A stream in western Tasmania - one of the habitats of *Sclerocyphon*. The surface flow patterns are revealed by time-lapse photography.

ASPECTS OF THE TAXONOMY, ECOLOGY AND HYDRODYNAMICS OF THE AUSTRALIAN PSEPHENIDAE (COLEOPTERA)

by

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This thesis contains no material which has been accepted for the award of any other degree or diploma except for sections of Chapter 2 (the historical review) and otherwise where stated herein. Sections of the historical review were included as part of the work required for B.Sc. (Hons) but have since been revised and rewritten.

To the best of my knowledge and belief it contains no copy or paraphrase of material previously published or written by another person except where due reference is made in the text.

J.A. Davis

20/1/82

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SUMMARY

Psephenid larvae (waterpennies) are well known members of the freshwater benthos, possessing a characteristic dorso-ventrally flattened shield. They are found clinging to rocks in rivers and streams that experience fast and turbulent flow regimes for at least part of the year. However, despite the fact that they occur in many of the rivers and streams of eastern Australia, and throughout Tasmania, very little study has been made of the family here.

Sclerocyphon is the only Australian genus of the Psephenidae. A brief review of the history of the Psephenidae, with particular emphasis on this genus and the subfamily encompassing it, the Eubriinae, is given.

Sclerocyphon comprises 12 species, six of which are described as new. Descriptions of six larval types representing discrete species but not, as yet, associated with adults, are also given. Re-descriptions of the genus and all previously described species are included as earlier workers possessed only limited material and features now considered to be of taxonomic importance, in particular, the male and female genitalia, were not described. Keys for the identification of both adults and larvae are given.

A major emphasis of the taxonomic study was on the association of adults and larvae and this was achieved mainly by laboratory breeding. Larvae are the dominant life history phase and fairly common while adults are much rarer.

The relative apomorphy or plesiomorphy of a number of larval characters is discussed and a phylogenetic classification of *Sclerocyphon*, based on larval characters, is proposed. Hinton's (1966) view of the Eubriinae as a subfamily (encompassing *Sclerocyphon*) of the Psephenidae, rather than Bertrand's (1972) concept of the Eubriinae as a separate family, is supported.

The distribution of each species and larval type is described and discussed with respect to present and some past environments in Australia. The complete endemism of the Tasmanian species of *Sclerocyphon* is considered to be a reflection of the low vagility of the genus and appears to be best explained by the vicariance model of historical biogeography.

A Gondwanaland origin of *Sclerocyphon* is suggested as it (or its nearest relative) occurs in Chile, as well as Australia, but nowhere else in the world. This disjunct southern distribution in a genus with low vagility is considered to be best explained by the vicariance of an ancestral Gondwanaland fauna.

Multivariate statistical techniques were used to investigate the shape of larvae of the Tasmanian species of *Sclerocyphon*. The most common Tasmanian species, *S. secretus*, was found to be the most variable, exhibiting a west-east trend in larval shape. Variation in larval shape was continuous with the widest, almost circular forms occurring on the west coast and the narrowest,most elongate forms on the east coast. Larval shape was found to be correlated with rainfall distribution, substrate and stream order. Contrary to expectations the narrowest, most elongate larvae were found to occur in streams of low mean velocity while wider forms occurred in streams of higher velocity. Three possible explanations for this paradox are given.

The second river and stream dwelling species in Tasmania, *S. aquaticus*, was found to be less variable in shape with larvae being predominantly wide and almost circular in form. The occurrence, and therefore the shape, of *S. aquaticus* larvae was found to be highly correlated with high stream order.

Flow visualisation techniques were used to investigate the hydrodynamics of larval *Sclerocyphon*. Dye trails revealed that all larvae are streamlined and inhabit a region of reduced flow immediately adjacent

to the substrate known as the laminar, or viscous, sublayer. The viscous sublayer exists within a thicker region of reduced flow associated with the substrate, the boundary layer, which, under most stream conditions, is turbulent.

Drag forces upon the larva are minimal while it remains within the viscous sublayer however respiratory exchange across this sublayer is limited to the slow rate of molecular diffusion. Larval *Sclerocyphon* overcome the constraints of this situation by creating their own respiratory current with a pair of anal, retractible, tracheal gills. During ventilation actively pumping gills create a turbulent area at the rear of the body which greatly enhances respiratory processes and waste removal. The gills also act as vortex generators, decreasing drag forces by controlling the larva's wake.

At high Reynolds number the thickness of the sublayer is reduced and larvae appear to employ a method of boundary layer control known, in fluid mechanics theory, as suction. The spaces between the lateral laminae act as slots through which a small amount of boundary layer fluid passes, creating a thinner but more stable boundary layer over the larva. This delays separation and therefore decreases the likelihood of the larva being swept off the substrate. For larvae of the Psepheninae and Eubrianacinae, which possess passive ventral tracheal gills, suction through slots between the lateral laminae may be the only means of maintaining adequate water flow over the gills.

Streamlining and associated boundary layer control allow larvae to move across substrates in high energy flows and to exploit the food sources there that are unavailable to other benthic invertebrates not possessing these hydrodynamic advantages.

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PART ONE

CHAPTER ONE

GENERAL INTRODUCTION

The Psephenidae are a small coleopteran family of cosmopolitan distribution occurring in Europe, North and South America, Africa, India, Asia and Australia. Their importance, in terms of species numbers, is relatively low as fewer than 100 species had been described by 1966 (Hinton, 1966) and only a very small number have been described since. However, the larvae (so-called waterpennies) which are found clinging to rocks in rivers and streams, are well-known members of the aquatic benthic invertebrate fauna. The dorso-ventrally flattened larvae are, in fact, a striking example of an aquatic insect form that has evolved extreme morphological adaptations to life in the lotic environment.

Despite their distinctive form the larvae are frequently mistaken for other animals, as illustrated by DeKay's description of two psephenid larvae as two new species of crustacean (DeKay, 1844 cited by Bertrand, 1939). The marked lack of association between the aquatic larvae and the terrestrial pupae and adults, combined with the inconspicuous habit of the latter two stages has resulted in a dearth of information on the systematics and biology of the family. The history of the classification of the family, with particular emphasis on the only Australian genus, *Sclerocyphon*, is given in Chapter 2.

The present taxonomic study of the Australian Psephenidae (Chapter 3) has evolved from a similar but much smaller study undertaken by the author as part of an Honours project (Davis, 1975). This early study was initiated partly in response to Britton's (1970, p.562) comments upon the state of knowledge of the Australian Psephenidae,

> "Psephenid larvae are common in mountain streams in south eastern Australia but have not yet been assoc-

> iated with adults..."

and

> "...no Australian species of Psephenidae have been described as such but *Sclerocyphon maculatus* Blackb. which was described as a helodid, is, in fact a psephenid."

These remarks highlighted the need for research on the family and, in particular, for a systematic study with major emphasis on the association of adults with larvae. The subsequent discovery of descriptions of seven species of *Sclerocyphon* for six of which larvae were not known (Blackburn, 1892; Lea, 1895, 1919; Carter, 1935) and 13 larval types for which adults were not known (Bertrand and Watts, 1965; Bertrand, 1969) further indicated the need to make such associations.

The earlier study (Davis, 1975) had been limited to a study of the taxonomy, life history and ecology of only two Tasmanian species of *Sclerocyphon*. However, a continuation of that study, encompassing a much larger number of Australian species, is presented here.

Traditionally, systematic entomology has been devoted to the description and classification of adults. Wiggins (1964) suggests that such an emphasis has been particularly detrimental to ecological studies in freshwater because a very large proportion of aquatic benthic communities consist of the immature stages of aquatic insects. The revision of *Sclerocyphon* presented here with its emphasis on larval taxonomy represents a partial remedy to this situation and should contribute to future ecological studies of Australian running waters.

Taxonomy alone, however, is not the sole objective of this study. Mayr (1969) notes that

> "...the making of a classification is not the end of the taxonomist's concern..."

and the taxonomic study described in Chapter 3 has acted as both the

foundation of, and catalyst for, research into a number of other aspects of psephenid biology.

The proposed phylogenetic classification (Chapter 3) together with information on the distributions of the various species provides the basis for the biogeographical study of the genus described in Chapter 4.

The earlier taxonomic study (Davis, 1975) also revealed the existence of considerable differences in larval shape, particularly between different populations within the Tasmanian species, *S. secretus*. A multivariate statistical analysis (described in Chapter 5) has been undertaken in an attempt to reveal the nature of variation and to define the possible influence of environmental factors on the expression of larval shape.

Murvosh's (1971) autecological study of the North American water-penny, *Psephenus herricki*, firmly established this species, and possibly all psephenid larvae, as inhabitants of the riffle zones of streams and rivers. Although a number of organisms live in riffle zones, and similar habitats, where the flow of water is a dominant factor, very few studies have investigated the effects of water velocity on animals at the size of an insect larva. The study of the interaction between organisms and their environment is the major goal of ecology and these interactions include the interplay between physical factors and morphology (Wainwright *et al.*, 1976). This, together with Hynes' (1970) suggestion that the flattened form of psephenid larvae enables them to live in the relatively slow moving boundary layer region around stones, inspired the study of the interaction between larval morphology and the benthic boundary layer described in Chapter 6.

This study of the hydrodynamics of psephenid larvae represents an attempt to explain observed biological phenomena in the light of the concepts and principles of fluid mechanics. It has become evident that fluid mechanics theory provides a valid framework in which to

examine the adaptations of aquatic invertebrates. On the other hand, examination of the form of an aquatic organism which has evolved in an environment in which water flow is a major selective factor may also be a means of exploring further aspects of fluid flow of interest to the student of fluid mechanics.

The overall aim of the studies described in this thesis was to contribute, if only in a small way, to the knowledge and understanding of freshwater ecosystems in Australia. Freshwater is a vital and much used resource in Australia and Watson (1981) suggests that,

> "...if any rational decisions are to be made on the future of Australian freshwater and the organisms they support, we urgently need more data on the organisms themselves."

Data on one of these organisms, *Sclerocyphon*, is presented here and hopefully provides a contribution towards the information that is needed for the rational management and ultimate preservation of Australian running waters.

CHAPTER TWO

HISTORICAL REVIEW OF THE PSEPHENIDAE

with particular emphasis on the Australian genus, *Sclerocyphon*, in the subfamily Eubriinae.

2.1 The Superfamilial Classification of the Psephenidae

Before any discussion of the psephenid genus (*Sclerocyphon*) studied here can take place it is necessary to review the historical treatment of the Psephenidae. Such a review must also encompass the superfamilies with which the Psephenidae have been associated because, although at the present time the Psephenidae are included within the Dryopoidea, some subfamilies and genera have previously been included in the Dascilloidea.

Holland (1972) noted that up to the present decade there has been considerable confusion and disagreement in the literature about systematics within the Dryopoidea. Initial confusion appears to have arisen from the fact that early classifications of the Psephenidae and associated groups were based only on a knowledge of adult characters.

According to Boving (1929), Leng (1920) in his *Catalogue of North American Coleoptera* recognised two series or superfamilies, the Dryopoidea and the Dascilloidea. The Dryopoidea contained the five families Psephenidae, Dryopidae, Helmidae, Heteroceridae, and Georyssidae. The Dascilloidea contained the three families Dascillidae, Helodidae, and Chelonariidae. Leng based his classification only on adult characters but stated that some of the genera of the Dascillidae may have to be removed to other families once their larvae were known.

After examination of larvae of the Dryopoidea and Dascilloidea, Boving (1929) found that a relationship existed between the two groups which indicated a need for reorganisation, as surmised by Leng. Boving (1929) examined the larvae of the dryopoid *Psephenus lecontei* (LeConte) (= *Psephenus herricki* (DeKay)) and the dascilloid *Eubrianax edwardsi* LeConte and found only minor differences between them. He therefore suggested that they should be included in one family, the Psephenidae, within the Dryopoidea. He also noted that the larvae of the above

two species were similar to the larvae of *Psephenoides gahani* Champion and *Helichus* sp., both of which belong to genera of the Dryopidae.

Boving and Craighead (1931) summarised the affinities of the genera which had been placed in the series Dryopoidea and Dascilloidea by Leng (1920) and on the basis of larval characters redefined the two series. They assigned the Chelonariidae, Lariidae, Ptilodactylidae, Dryopidae and Psephenidae to the Dryopoidea and the Heteroceridae, Dascillidae, Nosodendridae and Helodidae to the Dascilloidea. Although the newly defined series were no longer exactly comparable with the former ones they considered that the retention of the old names was desirable.

The Dryopoidea and the Dascilloidea have been retained as superfamilies by many workers, including Bues *et al.* (1954), Crowson (1955), Britton (1970) and Borror and DeLong (1970). They all include the Psephenidae, Dryopidae and Helminthidae in the Dryopoidea and the Dascillidae and Helodidae in the Dascilloidea. However, there is no such agreement on the placement of other families within the two superfamilies.

2.2 The Status of Subfamilies in the Psephenidae

Much debate has taken place on the status of the subfamilies included within the Psephenidae, in particular, on the Eubriinae (the subfamily encompassing *Sclerocyphon*) with some workers (noted below) maintaining that it should be recognised as a separate family, the Eubriidae.

The Psephenidae and the Eubriidae were established, on the basis of adult characters, by Lacordaire in 1854 and 1857, respectively. (Jeannel and Paulian, 1949). LeConte and Horn (1883) in *The Classification of the Coleoptera of North America*, recognised the family Parnidae (=Dryopidae) as comprising three very distinct subfamilies, the Parninae, the Psepheninae, and the Eliminae. The Psepheninae contained only one genus, *Psephenus*

LeConte. Within a second family, the Dascyllidae (= Dascillidae), they included two subfamilies, the Dascyllinae and the Helodinae. The latter was composed of five tribes, of which one was the Eubriini, containing the four genera, *Eubria* Latreille, *Ectopria* LeConte, *Dicranoselaphus* Guerain and *Acneus* Horn.

Pic (1914) in the *Catalogus Coleopterum* gave the two subfamilies, Dascillinae and Helodinae, familial status and divided the Helodidae into four subfamilies, one being the Eubriinae (Bertrand and Watts, 1965).

Boving and Craighead (1931) recognised the family Psephenidae and, as noted above, included both *Psephenus lecontei*, of the subfamily Psepheninae, and *Eubrianax edwardsi*, of the subfamily Eubrianacinae, within it, on the basis of larval characters. Hinton (1939), on the basis of a combination of adult and larval characters, extended the family Psephenidae to include a third subfamily, the Psephenoidinae. The genus *Psephenoides* Gahan had previously been placed by Gahan (1914), on the basis of adult characters, in LeConte and Horn's (1883) dascillid group, the Eubriini. Later, Boving (1929) assigned it to the Dryopidae on the basis of larval characters.

Following observations made by Bertrand (1939) on the life history of *Eubria palustris* Germar, Hinton (1955) incorporated a fourth subfamily, the Eubriinae, within the Psephenidae, once again on the basis of larval characters. Hinton (1955) noted that prior to the publication of Bertrand's (1939) observations, the larvae had been assigned to the Dryopidae, as Kellicott (1883) had described a larva of the Eubriinae as a species of the dryopid genus *Helichus*.

The first description of the larvae of the Psepheninae and the Eubriinae appear to have been given by DeKay in 1844 (Kellicott 1883, Bertrand 1939). DeKay (1844) described two new crustacean species *Fluvicola herricki* and *Fluvicola tuberculata*. LeConte (1850) realised

that these two species were actually insect larvae and redescribed the former as *Eurypalpus lecontei*. Kellicott (1883) re-named it *Psephenus lecontei* (LeConte). Bertrand (1939) recognised *Fluvicola tuberculata* as a member of the Eubriinae. Hinton (1955) realised that the two genera, *Helichus* and *Pelonomus*, previously placed in the Dryopidae, had been mis-identified and were, in fact, members of the Eubriinae, within the family Psephenidae.

As well as Hinton (1955), Crowson (1955) noted that on both larval and adult characters the genus *Eubria* and associated genera should belong to the Psephenidae. This interpretation has been followed by Britton (1970) and Brown (1976) who recognise the subfamily Eubriinae within the Psephenidae. However, other workers do not accept these views. Bradley (1947), Jeannel and Paulian (1949), Bertrand (1956) and Bertrand and Watts (1965) all recognise the Eubriinae as a separate family, the Eubriidae, and include it within the Dascilloidea. Bertrand (1972) recognises the Eubriidae, the Psephenidae and the Psephenoidinae as separate families and includes the Eubrianacinae as a subfamily in the Dascillidae.

From the discussion given above it can be seen that the status of the subfamily under consideration in this study, the Eubriinae, is still very much the subject of debate. In the present study, Hinton's (1955) classification of the Psephenidae as a family within the Dryopoidea, containing the four subfamilies, Psepheninae, Eubrianacinae, Psephenoidinae and Eubriinae, will be followed. The reasons for following this classification rather than Bertrand's (1972) classification of the Eubriidae as a separate family are discussed in Chapter 3.

2.3 Composition of Subfamilies within the Psephenidae

The Eubrianacinae and Psephenoidinae are the smallest subfamilies within the Psephenidae. The Eubranacinae contains only the genus

Eubrianax Kiesenweter while the Psephenoidinae contains two genera *Psephenoides* Gahan and *Afropsephenoides* Basilwesky.

The Psepheninae contains five genera, *Psephenus* Haldeman, *Mataeopseph⌣us* Waterhouse, *Psephenops* Grouvelle, *Xeranchorinus* Grouvelle, and *Tychespseph⌣us* Waterhouse. The latter three genera are little known, probably because they occur in the relatively unworked regions of South America. Further work on these three genera is needed for their true status within the Psephenidae to be determined.

The Eubriinae is the largest subfamily within the Psephenidae and contains the following eight genera; *Acneus* Horn, *Afroeubria* Bertrand, *Alabameubria* Brown, *Dicranoselaphus* Guerain, *Ectopria* LeConte, *Eubria* Latreille, *Sclerocyphon* Blackburn, and *Pelonomus* Boving and Craighead. A number of undescribed genera of the Eubriinae have also been recorded by Bertrand (1972).

The world distributions of these genera, in the four subfamilies, are illustrated and discussed in Chapter 4.

2.4 The Genus *Sclerocyphon*

In Australia the Psephenidae are represented only by the genus *Sclerocyphon*. Blackburn (1892) established the genus on a single small beetle found in the Victorian "alpine district". He named the specimen *Sclerocyphon maculatus* and assigned the new genus to the Malacodermidae, noting the resemblance of the type specimen to members of the helodid genus *Cyphon*. Pic (1914) included the genus *Sclerocyphon* within the Helodidae (Bertrand and Watts, 1965). Crowson (1955) removed *Sclerocyphon* from the Helodidae (superfamily Dascilloidea) and placed it in the subfamily Eubriinae (family Psephenidae; superfamily Dryopoidea).

According to Bertrand and Watts (1965) the occurrence of the Psephenidae in Australia was first recognised by Pic (1914) who described *Ectopria multinotata* and its variety, *E. multinotata* var. *robusta* from

Australia (locality unknown). The types of these species are held in the Pic Collection at Oxford. Bertrand and Watts (1965) noted that an examination of these type specimens by an Australian entomologist, Mr. J. Armstrong, revealed that they are actually *Sclerocyphon maculatus* Blackburn.

A checklist of the species of *Sclerocyphon* described prior to the present study is given in Table 2.1. All the species listed were described only on a knowledge of the adults, the pupal and larval phases apparently being unknown. However Carter (1935) noted that a single specimen of *S. irregularis* (=*S. maculatus*) was found in association with its pupal and larval cases. He provided an illustration of the adult with its pupal and larval exuviae but did not describe the exuviae. He noted the similarity of the larva to the larvae of the Dryopidae.

Hinton (1955) illustrated a larva and pupa of an unknown species of the Eubriinae from Tasmania and furnished details of the respiratory system of both.

Bertrand and Watts (1965) published the first review of the larvae of *Sclerocyphon* and stated that *Sclerocyphon* was a member of the family Eubriidae. They gave the first description of a larva and pupa of *Sclerocyphon* by describing the larval and pupal states of both *S. maculatus* and a new species designated *S. fuscus* Armstrong, *in litteris* (herein considered a *nomen nudum*). They also described larvae of five different types thought to represent previously unrecorded species. The larvae of one such type were linked with *S. aquaticus* by virtue of the fact that the larvae had been collected from the same Tasmanian localities as those from which adults of *S. aquaticus* had been recorded.

Hinton (1966) discussed respiratory adaptations of the pupae of *S. maculatus* and *S. fuscus* (*nomen nudum*).

Bertrand (1969) described the larvae of a further eight types, thought to represent unrecorded species of *Sclerocyphon*, from an

examination of specimens collected in Australia in 1966, by Professor J. Illies.

No further information on *Sclerocyphon* appears to have been recorded since 1969.

TABLE 2.1 Checklist of the Australian Psephenidae

Type Species

Sclerocyphon maculatus Blackburn, 1892 (Type) ... alpine district, Victoria.

synonyms:

Ectopria multinotata Pic, 1914, *E. multinotata* var. *robusta* Pic, 1914 ...locality unknown.

Sclerocyphon irregularis Carter, 1935 .....Belgrave and Warburton, Victoria. Dorrigo, New South Wales. NEW SYNONYMY

S. striatus Lea, 1895 .....Tamworth, New South Wales.

S. serratus Lea, 1895 .....Tamworth, New South Wales.

S. basicollis Lea, 1895 .....Tamworth, New South Wales.

S. aquaticus Carter, 1919 .....Waratah, Tasmania.

S. collaris (Fabricius), 1775 ....."nova Hollandia".

synonyms:

Tritoma collaris Fabricius, 1775 ....."nova Hollandia".

Sclerocyphon bicolor Carter, 1935 .....Kuranda and Endeavour River, Queensland.

CHAPTER THREE

TAXONOMY

Sclerocyphon lacustris sp.n.

3.1 Introduction

A clear need exists for a study of the systematics of the Psephenidae in Australia. Although the adults of seven* species of *Sclerocyphon* (the sole Australian genus) have been described (Chapter 2), the larvae of only one of these species; *Sclerocyphon maculatus*, is known. Furthermore, Bertrand and Watts (1965) and Bertrand (1969) have described a total of thirteen larval types which they are not able to associate with adults.

Difficulties in associating adults and larvae are at least partly due to the different habitat requirements of the life phases; the adults are terrestrial while the larvae are aquatic. Larvae are also more common, being present in rivers and streams throughout the year. The adults are much less often collected as they live for only a few weeks during the summer.

The emphasis of this study has been on associating larvae with adults and this has been achieved, for a number of species, mainly by rearing larvae to adulthood in the laboratory (Section 3.2).

Re-descriptions of all previously described species (except *S. serratus*, for which material was not available) are given (Section 3.4) as earlier workers possessed only limited material, sometimes of only one sex, and important features, in particular, the male and female genitalia, were not described. These re-descriptions are given first, in chronological order, followed by the descriptions of new species, arranged in alphabetical order. Traditionally insect species are described on the basis of adult features and this convention is followed in the present study. However, as the larva is the dominant life history phase of *Sclerocyphon* a detailed description of the larva (where known) is also included in both the re-descriptions and the

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* publication of an eighth species, *S. secretus* and additions to the description of *S. aquaticus* (Smith, 1981) came to hand too late for the format of this thesis to be changed. This paper and one other cited in this thesis (Smith and Dartnall, 1980) were written by the present author under her married name.

descriptions of new species.

Descriptions of six larval types representing discrete species but, as yet, not associated with adults, are also given (Section 3.4) as the information contained within these descriptions contributes much to the discussion of phylogeny and zoogeography in *Sclerocyphon*. Brown (1980) has created a precedent, with regard to larval types, by describing a new psephenid genus and species, *Alabameubria starki*, on the basis of larval features alone. He did this as the larva is very distinctive and the species appears to be extremely rare. No adults and only a few larvae were obtained, despite an intensive search, and so the likelihood of obtaining adults in the near future was also extremely low. Despite the fact that the six larval types of *Sclerocyphon*, noted above, are also distinctive they have not been named as new species as it is likely that adults will be obtained in the near future, either by field collection or laboratory rearing techniques. It is also probable that some of these larval types belong to species in which the adult has already been named (Section 3.4).

3.2 Materials and Methods

Collection, Rearing in the Laboratory and Sources of Loan Material

Larvae of *Sclerocyphon* were most efficiently collected by direct removal from rocks with fine forceps. They were placed immediately into a preservative solution of 70% ethanol and 5% glycerol. Live larvae were transferred from the field to the laboratory in stream water contained in plastic bags packed in ice. Leaves or twigs were included to provide surfaces to which the larvae could cling; rocks, which would crush the larvae, were not included.

Adults were often much more difficult to find because of their

cryptic behaviour. In contrast to some Australian mainland species, Tasmanian *Sclerocyphon* were not taken at light traps. No quick way of collecting these beetles was found. The litter, grass, rocks and debris of river banks were searched by hand and adults removed with fine forceps or an aspirator. Adults were most commonly found in high water leaf packs or amongst riparian grass tussocks. Occasionally beetles were seen on the wing and, in all cases, those beetles actually landed on the collector, or nearby rocks, and were taken by hand. However, the beating of the riparian vegetation with nets failed to capture any beetles.

Adults were preserved in a solution of 70% ethanol and 5% glycerol or pinned and dried. The small size and brittle nature of dried specimens often resulted in damage during subsequent examinations so in the present study the majority of adults were preserved in the ethanol/glycerol solution.

In the present study most of the adults were obtained by rearing larvae to adulthood in the laboratory. Two methods were used. Adults of the three Tasmanian species: *S. aquaticus*, *S. lacustris* sp.n., and *S. secretus* sp.n., were obtained by keeping larvae, from various localities, in the laboratory under simulated stream conditions. Tanks were set up with constantly circulating stream water at 17-18°C and lit for 14 hours a day. One large tank, designed by Dr. J.L. Hickman, Zoology Department, University of Tasmania (Plate 3.1) and six small tanks were used. The smaller tanks were all similarly constructed, as illustrated in Figure 3.1, with a deep pool acting as a reservoir at one end, a middle sloping section representing a riffle and a shallow pool at the other end. Water circulated constantly, entering near the base of the deep pool and overflowing down the riffle to the shallow pool from where it was recirculated by a centrifugal pump. An aerator was placed in the deep pool to ensure adequate aeration. A bank was constructed on

PLATE 3.1 Large fibreglass tank used to simulate stream conditions for the rearing of larvae to adulthood in the laboratory. Length of tank; 155 cms. Width of tank; 65 cms.

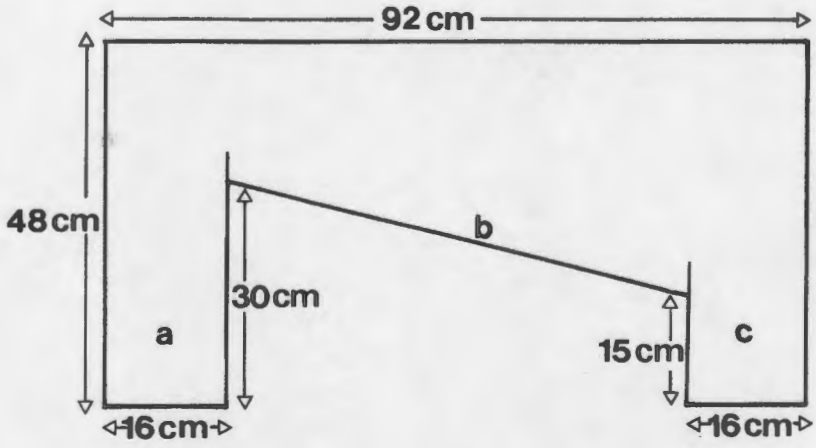


FIGURE 3.1 Side view of small fibreglass tank used to simulate stream conditions, for the rearing of larvae to adulthood, in the laboratory. a = upstream reservoir, b = riffle, c = down-

each side of the middle section using rocks, earth and moss and it was here that pupation and emergence took place. From larvae reared in these tanks adults were obtained several months earlier than their first occurrence in the field.

The second method used was much simpler and proved particularly useful for rearing adults of the Australian mainland species. Last instar larvae of these species were transported to Tasmania in sealed Petri dishes (10 cm in diameter) containing damp moss, or in some cases, damp sponge. Larvae were then transferred to larger containers (14 cm × 14 cm × 16 cm) with damp earth, moss and pebbles. Containers were sealed, apart from small air holes, so that the relative humidity remained high. Pupation and adult emergence took place within these containers. Adults of *S. maculatus*, *S. basicollis*, *S. striatus*, *S. armstrongi* sp.n. and *S. zwicki* sp.n. were successfully obtained in this way. The disadvantage of this method was that for pupation to occur last instar larvae needed to be fairly mature when placed in the container. In contrast, even larvae of earlier instars placed in the recirculating tank system would proceed to emergence.

Larval, pupal and adult material from a number of collections were examined. Abbreviations for the various institutions which supplied material from their collections are, as follows: ANIC, Australian National Insect Collection, CSIRO, Canberra; BMNH, British Museum (Natural History), London; BPBM, Bernice P. Bishop Museum, Honolulu; CIT, Caulfield Institute of Technology, Melbourne; JCUNQ, James Cook University of North Queensland, Townsville; MMBW, Melbourne Metropolitan Board of Works, Melbourne; NMV, National Museum of Victoria, Melbourne; NMV-SD, National Museum of Victoria Survey Department, Melbourne; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; TM, Tasmanian Museum and Art Gallery, Hobart; EDUQ, Entomology Department, University of Queensland, St. Lucia.

In addition a number of people kindly made their personal collections available for study. The largest of these collections are identified by the following abbreviations of the owners' names: CW, Dr. C. Watts, Institute of Medical and Veterinary Science, Adelaide; PZ, Dr. P. Zwick, Max Planck Institute for Limnology, Schlitz, Austria; and WDW, Professor W.D. Williams, University of Adelaide, Adelaide.

The collection supplied by Dr. C. Watts had been the basis for a previous systematic work on larval *Sclerocyphon* (Bertrand and Watts, 1965). Examination of this collection facilitated interpretation of the work. Comparison of *Sclerocyphon* with the Psepheninae was greatly aided by the examination of Canadian specimens of *Psephenus herricki* made available by Professor H.B.N. Hynes of the University of Waterloo, Ontario, Canada.

Examination, Dissection and Illustration

Larvae were examined, in 70% ethanol, with an MC6-1 stereomicroscope. Dried adults were temporarily pinned on polystyrene foam for examination. Adults preserved in ethanol were examined wet or else made comparable with pinned material by superficial drying in air, on absorbent paper, for approximately 15 minutes prior to examination. Adults treated in this way could be returned to ethanol after examination. All measurements were made with an MC6-1 stereomicroscope fitted with an 8X eyepiece graticule.

Temporary mounts were made of adult and larval appendages. To obtain the external genitalia of adults the last two abdominal sclerites were removed and the genitalia gently dissected out using a microscalpel and mounted entomological pins. In many males the aedeagus was everted upon death and so could be easily removed with forceps without actual dissection. Where possible, dissection of paratype, rather than holotype,

genitalia was carried out to minimize the damage to holotype material. Genitalia were cleaned and cleared by soaking in a hot solution of dilute potassium hydroxide (10% KOH) for thirty minutes, then mounted in glycerol. Temporary rather than permanent mounts were made so that the genitalia could be manipulated for viewing in various aspects.

Drawings of genitalia and appendages were made using a Leitz Prado microprojector attachment on a Leitz Pradovit 250 slide projector. Drawings of whole animals, adults and larvae, were first made with a Wild *camera lucida* mounted on a Wild MS stereomicroscope. As use of the *camera lucida* did not allow the inclusion of many of the finer details these were added from an examination of photographs of specimens taken by Mr. D. Peacock, Photographic Department, University of Tasmania. Final drawings of both whole animals and genitalia were corrected for symmetry and copied onto drafting film using Staedtler Mars 700H pens, indian ink and scalpel blades (the pubescence of the beetles was reproduced with a scraping technique).

Larvae of all species, except *S.* type E and *S.* type F (of which insufficient material was available), were examined with a Jeol JXA-50A scanning electron microscope in the Central Science Laboratory of the University of Tasmania. Plates of important features were produced with a Polaroid 200 Land camera.

3.3 Morphology

To facilitate the use of adult and larval keys, and the interpretation of species descriptions, labelled diagrams of a representative *Sclerocyphon* beetle (dorsal and ventral views), the male and female genitalia (dorsal views) and the larva (dorsal view) (Figures 3.2-3.6) are provided. The terminology used in the description of beetles follows that given by Brown (1976) for aquatic dryopoid beetles while

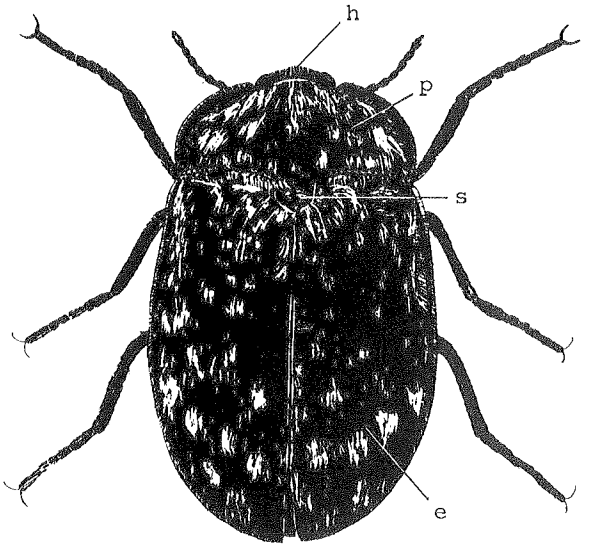
Key to structures of *Sclerocyphon*

Adults

h	head
p	pronotum
s	scutellum
e	elytra
pr	prosternum
m	mesosternum
me	metasternum
as	abdominal sternites
he	hemisternites
st	styli
r	rod (sclerotised) embedded in ventral vaginal wall
pl	plates (sclerotised) embedded in anterior vaginal wall
lat fr	lateral frame
bas p	basal piece
par	parameres
dps	dorsal penile sclerite
vps	ventral penile sclerite

Larvae

mfo	marginal fringe - outer band
mfi	marginal fringe - inner band
pi	pits
mcts	mucous-coated trichoid sensilla
gt	gin trap
cb	cuticular bead
es	ecdysial scar
sp	spiracle
sp b	spiracular brush
pro	pronotum
mes	mesonotum
met	metanotum
t1-t9	tergites 1-9



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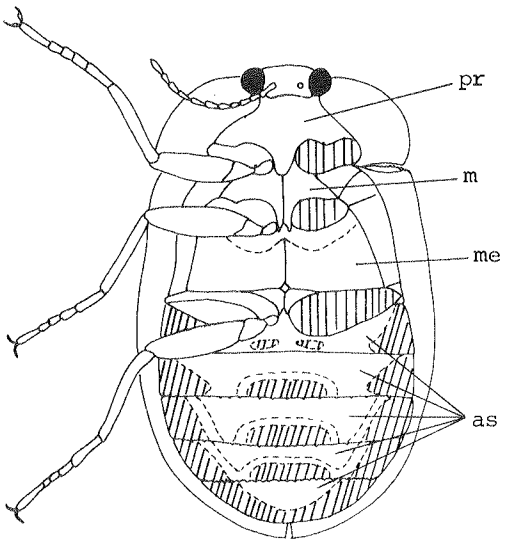

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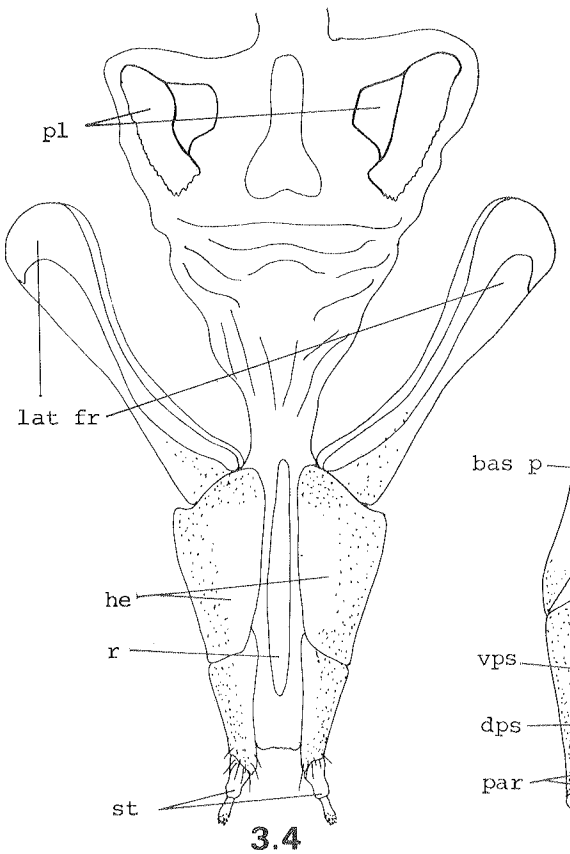

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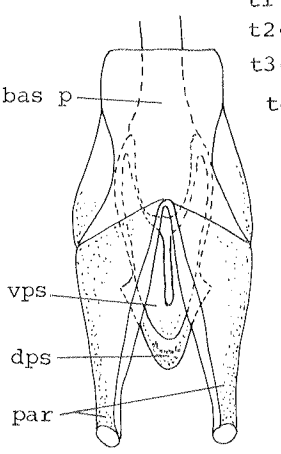

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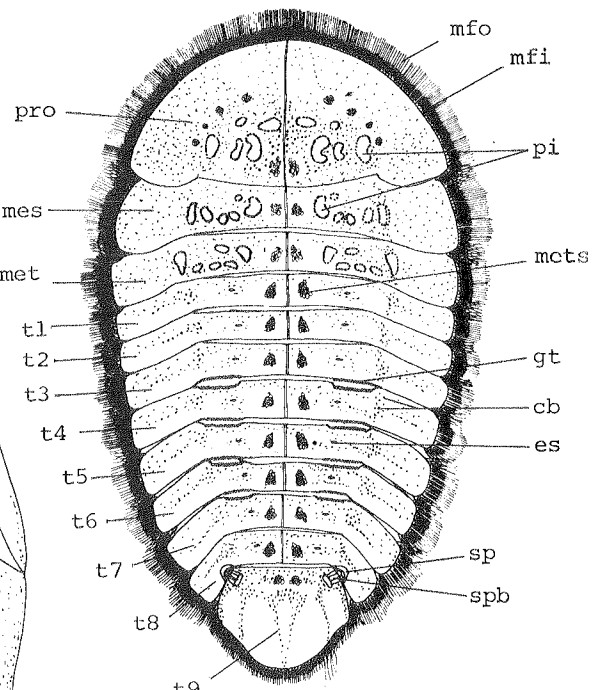


3.6

FIGURES 3.2-3.6 Diagrams showing structures of a representative *Sclerocyphon* beetle and last instar larva: (3.2) ♀ dorsal view; (3.3) ♀, ventral view; (3.4) ♀, external genitalia, ventral view; (3.5) ♂ genitalia, ventral view; (3.6) last instar larva, dorsal view.

the terminology used in the description of the genitalia follows that of Tuxen (1970). The terminology used in the description of larvae is after Bertrand and Watts (1965).

3.4 Systematics

Key to the Species of *Sclerocyphon* in Australia.

1 Metasternum with posterior margin produced in shallow curve each side of mid-ventral line, behind antecoxal piece (Figure 3.30)

S. aquaticus

Elongate beetle, 5-7 mm in length, elytra "waisted", dorsal penile sclerite (Figure 3.7a) long, tapered, vaginal plates as in Figure 3.8a. Endemic to Tasmania

Figures 3.29-2.32

Metasternum with posterior margin straight behind antecoxal piece 2

2(1) Dorsal penile sclerite with two lateral projections or barbs (Figure 3.7b), vaginal plates with prolonged lateral extensions on inner edge (Figure 3.8b)

S. secretus

Elongate beetle, 4-6 mm in length, dorsal surface with small clumps of white pubescence. Endemic to Tasmania. Figures 3.34-3.37

Dorsal penile sclerite without two lateral projections or barbs, vaginal plates without prolonged lateral extensions 3

3(2) Dorsal penile sclerite (Figure 3.7c) large, 0.7 mm in length, 0.3 mm in width, widest just before base, tapering to rounded apex, vaginal plates (Figure 3.8c) expanded and convoluted anteriorly, 0.4 mm in length, 0.25 mm in width (anterior). Beetle from Tasmania

S. lacustris

Elongate beetle, 5-6 mm in length, derm moderately shining beneath dense fine ashen pubescence, usually uniformly dark brown. Endemic to Tasmania. Figures 3.52-3.55

Dorsal penile sclerite not as above, vaginal plates not as above. Beetle from mainland Australia.....4

4(3) Broad, subconvex ovate beetles.....5

Not as above, elongate-elliptic or convex, almost circular beetles.....6

5(4) Elytral striae obvious, marked by longitudinal rows of white pubescence. Dorsal penile sclerite long (0.6 mm), tapering to very narrow apex (0.3 mm wide at base, 0.05 mm wide at apex) (Figure 3.7d). Form of vaginal plates not known.

S. aquilonius

Beetle usually dark brown with some yellow, 5.5-8 mm in length. Northern Queensland. Figures 3.43 - 3.46.

Elytral striae only visible in lateral and apical regions. Dorsal penile sclerite long (0.75 mm) tapering to blunt apex (0.3 mm wide at base, 0.1 mm wide at apex) (Figure 3.7e). Vaginal plates elongate, narrow (0.38 mm x 0.13 mm) (Figure 3.8d).

S. zwicki

Beetle usually dark brown-black with red-yellow patches, 5.5-8 mm in length. Victoria and N.S.W. Figures 3.66-3.69

6(4) Elongate-elliptic, subconvex beetles with dense covering of fine pubescence, plus clumps of coarse white pubescence, over moderately shining derm.....7

Almost circular or ovate, convex beetles with variable covering of fine pubescence over very shiny derm.....8

7(6) Elytral striae obvious, marked by longitudinal rows of white pubescence. Dorsal penile sclerite (Figure 3.7f) narrow elongate (0.45 mm x 0.17 mm), vaginal plates (Figure 3.8e) small, anteriorly widened (0.22 mm in length, 0.15 mm in width, anteriorly).

S. armstrongi

Beetle usually dark brown, 4-5.5 mm in length, S.A. and western Victoria. Figures 3.47-3.50

Elytral striae not obvious medially but visible apically and laterally. Striae not marked with pubescence but dense covering of pubescence over entire elytra. Ventral penile sclerite (Figure 3.7g) with slight barb each side of apex, dorsal penile sclerite (Figure 3.7g) 0.5 mm in length, 0.25 mm wide at base. Vaginal plates (Figure 3.8f) prolonged at outer anterior edge (0.3 mm x 0.15 mm).

S. striatus

Beetle usually dark brown with red-yellow patches, 3.5-5.5 mm in length. Victoria and N.S.W. Figures 3.15-3.18

8(6) Pronotum with medial third black, lateral third on each side yellow. Elytra "waisted". Dorsal penile sclerite (Figure 3.7h) 0.45 mm in length, 0.25 mm wide near base. Vaginal plates (Figure 3.8g) small with narrow projection

at outer anterior edge (0.18 mm x 0.15 mm)

S. collaris

Extremely shiny beetle, elytra usually black, 4-5.5 mm in length. Queensland. Figures 3.25-3.28.

Not as above.....9

9(8) Elytra broad and convex relative to pronotum, greatest height and width at middle. Dorsal penile sclerite (Figure 3.7i) 0.5 mm in length, 0.25 mm in width near base. Vaginal plates (Figure 3.8h) elongate, 0.4 mm in length, anterior outer edge extended.

S. nitidus

Extremely shiny beetle, usually black with red-yellow patches, elytral margins wide, flattened 4.4-6.5 mm in length. Queensland, N.S.W. Figures 3.62-3.65

Not as above.....10

10(9) Oval, convex beetle with elytra swollen in apical third. Dorsal penile sclerite (Figure 3.7j) 0.6 mm in length, 0.22 mm in width near base. Vaginal plates (Figure 3.8h) 0.3 mm in length, widely expanded anteriorly.

S. maculatus

Beetle usually dark brown-black with red-yellow patches. Dense patches of coarse white pubescence on dorsal surface plus glabrous shining regions. 4-5 mm in length. Victoria and N.S.W. Figures 3.10-3.13

Not as above.....11

11(10) Narrow ovate beetle with one or two crescent-shaped glabrous regions each side of elytral suture. Dorsal penile sclerite (Figure 3.7k) 0.4 mm in length, 0.25 mm in width near base. Vaginal plates (Figure 3.8j) with long, narrow apex, anterior margin highly convoluted, 0.4 mm in length, 0.18 mm in width (anterior).

S. minimus

Small beetles, 3-4 mm in length, usually light brown or brown. Male with midline parting in pubescence on sternites 2 and 3, sternite 3 produced in curve posteriorly, each side of midline. Queensland and N.S.W. Figures 3.57-3.61

Almost circular beetle without crescent-shaped glabrous regions as above. Dorsal penile sclerite (Figure 3.7ℓ) very short, 0.35 mm in length, 0.2 mm in width, at base. Vaginal plates (Figure 3.8b) short and narrow, 0.25 mm in length, 0.15 mm in width (anterior).

S. basicollis

Small beetles, 3-4 mm in length, usually black, sometimes with red-yellow patches, very fine white pubescence (often abraded) over shining derm. Victoria, N.S.W., Queensland. Figures 3.20-3.23

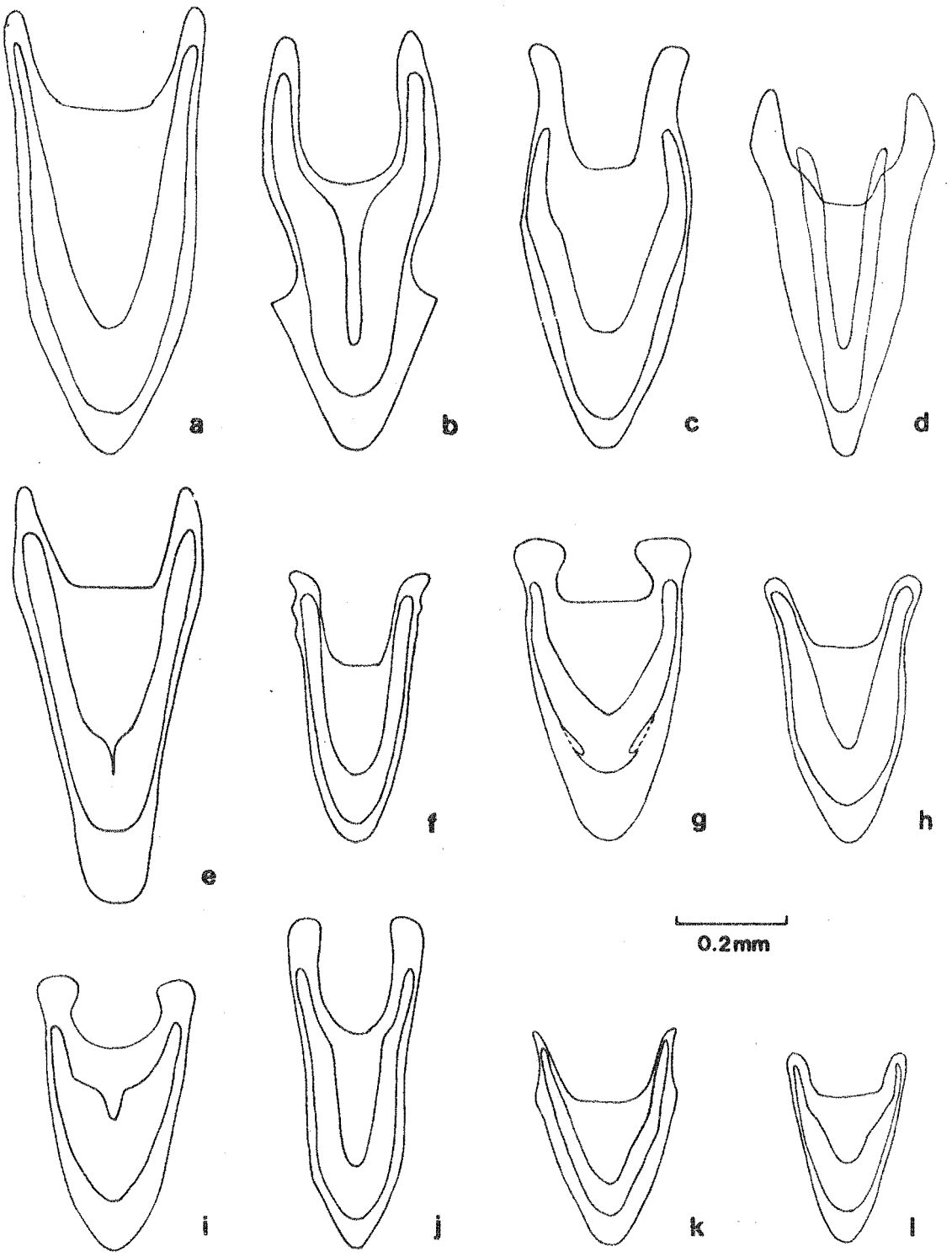


FIGURE 3.7 *Sclerocyphon*, ♂, ventral and dorsal penile sclerites, ventral view:
(a) *S. aquaticus;* (b) *S. secretus;* (c) *S. lacustris;* (d) *S. aquilonius;* (e) *S. zwicki;* (f) *S. armstrongi;* (g) *S. striatus;* (h) *S. collaris;* (i) *S. nitidus;* (j) *S. maculatus;* (k) *S. minimus;* (l) *S. basicollis.* Scale line = 0.2 mm.

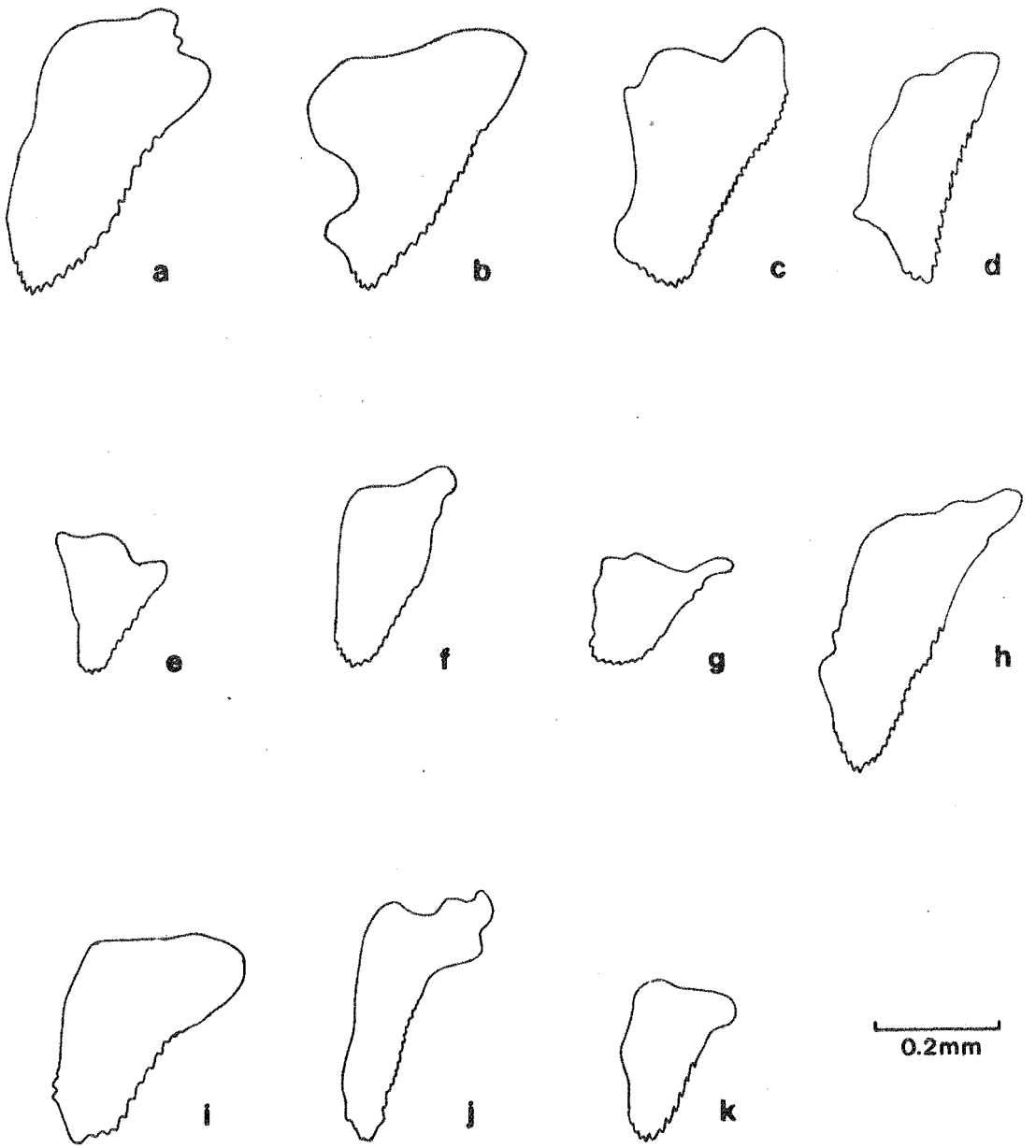


FIGURE 3.8 *Sclerocyphon*, ♀, plate embedded in left wall of vagina, ventral view:
(a) *S. aquaticus;* (b) *S. secretus;* (c) *S. lacustris;*
(d) *S. zwicki;* (e) *S. armstrongi;* (f) *S. striatus;*
(g) *S. collaris;* (h) *S. nitidus;* (i) *S. maculatus;*
(j) *S. minimus;* (k) *S. basicollis.* Scale line = 0.2 mm.

Key to Last Instar Larvae of *Sclerocyphon* in Australia.

1 Dorsal surface with 2 gin traps on adjoining margins of tergites 3-4, 4-5.

S. type E

N.S.W. Figures 3.9a, 3.75.

Dorsal surface with more than 2 gin traps.....2

2(1) Dorsal surface with 3 gin traps on adjoining margins of tergites 3-4, 4-5, 5-6.....3

Dorsal surface with 4 gin traps on adjoining margins of tergites 3-4, 4-5, 5-6 and 6-7.....9

3(2) Tergite 9 with 3 longitudinal ridges.....4

Tergite 9 without 3 longitudinal ridges.....8

4(3) Tergite 9 with 3 strongly upraised longitudinal ridges all extending to posterior margin.....5

Tergite 9 with 3 weak longitudinal ridges, central ridge not raised beyond middle.....7

5(4) Tergite 9 (Figure 3.9b) nearly rectangular in outline, posterior margin produced in shallow curve, central ridge upraised, tapered shining. Dorsal shield with longitudinal row of black setae each side of midline, lateral laminae with transverse row of short black setae.

S. zwicki

Victoria, N.S.W. Figures 3.9b, 3.70. Pls 3.28-3.30

Tergite 9 not as above, dorsal shield without longitudinal row of black setae each side of midline and transverse rows

on lateral laminae.....6

6(5) Tergite 9 (Figure 3.9c) with central ridge wide, tapered, strongly upraised, all 3 ridges densely covered by cuticular beads. Posterior margin with 4 sinuosities and rounded or pointed apex. Mid-dorsal sensilla in shining circular mucus-coated clumps.

S. striatus

Victoria, N.S.W. Figures 3.9c, 3.19. Pls 3.5-3.9

Tergite 9 (Figure 3.9d) with central ridge narrow, all 3 ridges sparsely covered with cuticular beads. Posterior margin with weak sinuosities and rounded or pointed apex. Mid-dorsal sensilla in small, upraised, mucus-coated clumps.

S. type C

Queensland, N.S.W. Figures 3.9d, 3.73. Pls 3.40-3.44

7(5) Tergite 9 (Figure 3.9e) with 3 weak ridges outlined by cuticular beads, posterior margin flattened, beads sparse. Dorsal shield with 2 rows of cuticular beads across tergites 1-8, anterior row extending down each lateral lamina to middle. Mid-dorsal sensilla in grey, shining, mucus-coated clumps (visible as discrete spathulate sensilla with ornately sculptured mucous coats under scanning electron microscopy). Many small regions of grey shining mucus over entire shield.

S. type B

Queensland. Figures 3.9e, 3.72. Pls 3.34-3.39

Tergite 9 (Figure 3.9f) with 3 weak ridges covered with cuticular beads. Posterior margin not as above. Cuticular beads on dorsal shield not as above. Mid-dorsal

sensilla in shining, circular mucus-coated clumps (sensilla not sculptured as above) outlined by ring of shining yellow pores. Numerous shining yellow pores over entire shield.

S. basicollis

Victoria, N.S.W., Queensland. Figures 3.9f, 3.24. Pls 3.10-3.12

8(3) Tergite 9 (Figure 3.9g) nearly triangular in outline, posterior margin produced in shallow curve medially, bordered each side by shallow concavity. Cuticular beads largest and densest at base, smaller and sparser at posterior margin. Shining mucus-coated "Y"-shaped region at base. Mid-dorsal sensilla in shining mucus-coated elliptical clumps.

S. armstrongi

S.A. and Victoria. Figures 3.9g, 3.51. Pls 3.21-3.24

Tergite 9 (Figure 3.9h) broadly triangular in outline, posterior margin shallowly curved. Grey, shining, often diamond-shaped mucous mass at base. Mid-dorsal sensilla in shining mucus-coated oval clumps.

S. type F

Queensland and N.S.W. Figures 3.9h, 3.76

9(2) Four gin traps with only lower margin of each sclerotised, giving 4 "half" gin traps. Tergite 9 (Figure 3.9i) broadly triangular in outline, lacking upraised ridges, densely covered with cuticular beads. Mid-dorsal sensilla in shining inverted "Y"-shaped mucus-coated clumps.

S. maculatus

Victoria and N.S.W. Figures 3.9i, 3.14. Pls 3.2-3.4

Four gin traps with both lower and upper margins sclerotised. Tergite 9 not as above. Mid-dorsal sensilla not as above.....10

10(9) Tergite 9 (Figure 3.9j) lacking ridges but fine transverse folds present. Entire medial region shining, lacking cuticular beads. A longitudinal pit at the junction of body and each lamina.

S. type A

Queensland. Figures 3.9j, 3.71. Pls 3.31-3.33

Tergite 9 not as above. Medial region with cuticular beads. No longitudinal pits at junction of body and each lamina.....11

11(10) Tergite 9 (Figure 3.9k) with 3 narrow upraised longitudinal ridges covered with cuticular beads. Posterior margin with 4 sinuousities and pointed apex. Mid-dorsal sensilla in grey shining mucus-coated clumps.

S. type D

Queensland. Figures 3.9k, 3.74. Pls 3.45-3.50

Tergite 9 not as above.....12

12(11) Tergite 9 (Figure 3.9ℓ) nearly square in outline, posterior margin produced in shallow curve. Three weak ridges with central ridge wide, tapered, shining. Medial region with long black setae in pores each side of midline, some with grey mass of mucus at base, setae sometimes absent (abraded) leaving shining pores visible. Lateral laminae with transverse row of short black setae.

S. aquaticus

Tasmania. Figures 3.9ℓ, 3.33. Pls 3.13-3.15

Tergite 9 not as above, posterior margin with small or large sinuosities, medial region without black setae. Lateral laminae without transverse row of short black setae.....13

13(12) Tergite 9 (Figure 3.9m) with posterior margin produced in semi-circle medially, apex rounded or pointed, a slight sinuosity each side of middle. Three upraised ridges with central ridge extending to posterior margin. Mid-dorsal sensilla in elongate-oval mucus-coated clumps.

S. secretus

Tasmania. Figures 3.9m, 3.38-3.42. Pls 3.16-3.20

Tergite 9 (Figure 3.9n) with posterior margin produced in deep semi-circle medially with a large shallow sinuosity on each side. Three weak ridges, central ridge not extending beyond middle. Mid-dorsal sensilla visible as discrete mucus-coated projections in oval clumps. Fine setae extending from pores over much of shield.

S. lacustris

Tasmania. Figures 3.9n, 3.56. Pls 3.25-3.27

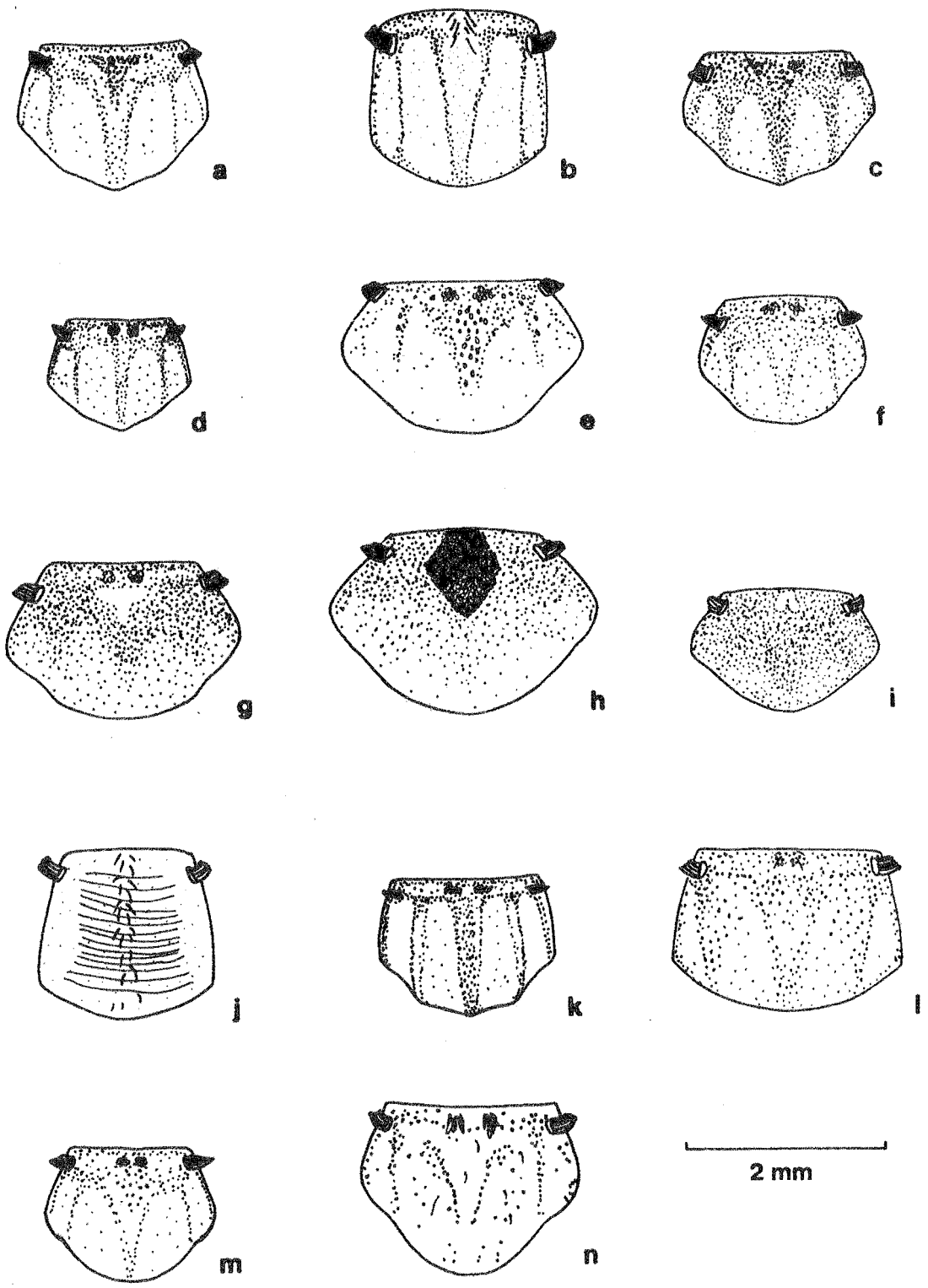


FIGURE 3.9 *Sclerocyphon*, last instar larva, tergite 9: (a) type E; (b) *S. zwicki*; (c) *S. striatus*; (d) *S.* type C; (e) *S.* type B; (f) *S. basicollis*; (g) *S. armstrongi*; (h) *S.* type F; (i) *S. maculatus*; (j) *S.* type A; (k) *S.* type D; (l) *S. aquaticus*; (m) *S. secretus*; (n) *S. lacustris*. Scale line = 2 mm.

Genus *Sclerocyphon* Blackburn

Sclerocyphon Blackburn, 1892, p.522

Type species: *Sclerocyphon maculatus* Blackburn 1892

Description

Adult

As given by Blackburn (1892) but with the following additions:

Small convex-subconvex beetles, densely minutely punctate overall. Entire ventral surface, head and legs clothed with short dense pubescence. Dorsal surface with variable pubescence.

Head deflexed, partly enclosed by emarginate pronotum, eyes rounded, antennae with segments 1-2 relatively glabrous, shining, yellow, remainder dark, covered with dense pubescence, segments 3-7 triangularly compressed, segments 8-11 filiform.

Clypeus prolonged forwards between fairly close antennal insertions, labrum and mandibles hidden beneath. Labrum small, mandibles small, sub-triangular. Maxillae 4-segmented, distal segment expanded, triangularly compressed with minute apical projections, palpifer relatively large, stipe small, galea and lacinia fused as 3 plumose setaceous tufts, long fine setae over entire maxillae. Labial palps 3-segmented, expanded, triangularly compressed with minute apical projections, ligula consisting of 4 plumose setaceous tufts corresponding to paraglossae and glossae.

Pronotum strongly transverse, lateral margins explanate, apical angles prominent. Posterior margin of pronotum and anterior margin of elytra and scutellum crenulate.

Scutellum widely arcuately triangular.

Elytra with short longitudinal impression on anterior margin, one third distance from scutellum, on each side. Shoulders gently

tuberculate. Transverse marginal impression below shoulder on each side.

Prosternum strongly produced into narrow posterior projection. Mesosternum fairly flat, excised anteriorly for reception of prosternal process, produced posteriorly into narrow curved projection each side of midline. Metasternum fairly flat.

Fore-legs with coxae separate, produced transversely for reception of femur, trochantin visible, femur with groove for reception of tibia, undersurface glabrous. Tibia with 2, extremely reduced, apical spines. Tarsi almost length of tibia, 5-segmented, not lobed, $1>2>3>4\leq5$, $5\leq2+3+4$, tarsal claw bifid, inner margin lightly dentate. Mid-legs as fore but transverse production of coxae considerably less, no groove for reception of femur. Hind-legs as fore but coxae larger, narrowly transversely produced with deep groove for reception of femur, femur somewhat flattened.

Abdomen with 5 visible sternites, posterior margins of sternites 2 and 3 fairly serrate, sternite 4 strongly serrate.

♂ external genitalia with aedeagus symmetrical, trilobate. Basal piece spinose proximally, membranous except for narrow chitinised lateral plates. Parameres large, sclerotised, punctate, with membranous tips. Penis complex, consisting of 2 sclerites, dorsal sclerite larger, curved downwards at tip, ventral sclerite smaller. Ejaculatory duct opening at base of 2 sclerites, internal sac undifferentiated.

♀ with pair of chitinised hemisternites, lightly punctate, distal portion setose, bearing 2-segmented styli, proximal segment membranous, distal segment sclerotised with membranous tip bearing minute apical projections. Sclerotised rod embedded in ventral vaginal wall between hemisternites. Proximal region of vagina supported by lateral frame, sclerotised ventrally, articulating at base with hemisternites. Two sclerotised plates embedded in anterior latero-dorsal wall of vagina covered with minute trinagular teeth, largest and densest at

outer edge, smaller, sparser in inner region.

Last instar larva

Description as given by Bertrand and Watts (1965) but with the following additions:

Thoracic and abdominal segments forming shield completely hiding head and legs from above, dorso-ventrally flattened. Entire marginal fringe present on lateral and posterior margins of lateral laminae, pronotal shield and posterior margin of ninth tergite. Pronotum forming regular semi-circular shield in front. Lateral laminae of meta- and mesonotum and tergites 1-8 broad, flattened, each in close approximation to anterior and posterior laminae. Ninth tergite with lateral margins facing the posterior margins of lateral laminae of eighth tergite and with posterior margin closing the entire thoraco-abdominal shield at the posterior end.

Pro-, meta- and mesonotum with a number of pits in constant pattern each side of midline.

Twelve paired groups of shining mucus-coated trichoid sensilla present in medial region of dorsal surface, one group each side of midline on each thoracic and abdominal segment or a longitudinal row of long black setae each side of midline on each thoracic and abdominal segment.

Two, three or four pairs of gin traps on dorsal surface consisting of sclerotic bands on post-scutellum region of one segment and on the adjoining pre-scutellum region of following segment on segments 3-4, 4-5 (two pairs), 5-6 (3 pairs) and 6-7 (4 pairs).

One pair of functional spiracles present on posterior lateral margin of eighth tergite, close to junction with posterior margin, a 'spiracular brush', associated with each spiracle, present on the adjoining anterior/lateral margins of the ninth tergite, spiracular brush consisting of tuft of setae, on a small protusion, closing over the

spiracular opening.

Head hidden from above, globular in front, retractable in a pocket between the prosternal shield and prosternal sclerites, usually directed forwards but movable in all directions. Antennae three-segmented, first two almost equally developed, first more robust and slightly curved, third greatly reduced in size. Ocelli one group present on each side of head, consisting of six lenses, a little unequal in size, lying close together over one dark pigment spot. Clypeus membranous, some hairs present on anterior margin. Labrum quadrangular with rounded corners distal area covered with short, palmate hairs, covers mouthparts but semi-transparent with mandibles visible beneath. Mandibles heavily chitinised, two forms occurring, longitudinally elongate, triangular type most common, very short sub-triangular type sometimes present, internal face concave, distal area with fissures but no teeth, long prostheca plus a long plumose seta present in hollow of the internal face. Maxillae 3-segmented maxillary palps, distal segment with minute apical projections and one branched seta, palpiger with one stiff seta, second segment with three finely branched setae, stipe with branched setae plus three stiff bristles on lateral margin, lacinia and galea largely fused, galea small with several short branched setae laterally and denser curved spines dorsally, both longer whole spines and shorter serrated ones present, lacinia spathulate, convex medial edge with two rows of strong apically bent spines, increasing in length distally, both whole and serrated, stout, heavily chitinised apical spine present. Labium elaborate in structure, mentum doubtfully distinct from palpi bearing distal portion, dorsal surface leading straight into oral cavity, 2-segmented labial palps, distal segment with minute apical projections, proximal segment with three finely branching setae, paraglossae and glossae appearing fused, densely covered with palmate setae, containing group of finely

branched setae in distal and medial lateral regions, one pair of very long, simple setae present, two groups of small rounded bead-like cuticular projections present, proximal lateral margins with varying number of stiff setae, 2-4.

Legs short, plump, only slightly movable, 5-segmented, coxal cavities broadly separated, coxa large, widened, trochanter large, femur flattened with one long seta projecting dorsally, tibio-tarsus half the length of femur, carrying a single, strong, chitinised, moderately curved claw, swollen at base and approximately half the length of tibio-tarsus, each claw with a slender interior spine, apical region of tibio-tarsus with long setae projecting both anteriorly and posteriorly, posterior margin with second clump of stiff setae, all segments with short, stiff setae.

Ventral sclerite of ninth abdominal segment forming an operculum covering an ano-branchial cloaca containing two retractable anal gill tufts, a pair of anal papillae and anus.

Sclerocyphon maculatus Blackburn

(Figures 3.10-3.14, Pls 3.2-3.4)

Sclerocyphon maculatus Blackburn, 1892, p.522

Ectopria multinotata Pic, 1924, p.31

Sclerocyphon irregularis Carter, 1935, p.190. NEW SYNONYMY

Material Examined

Types - VICTORIA: holotype ♂ (?), alpine district, BMNH; holotype ♀ of *S. irregularis* (with pupal and larval exuviae, on card), Belgrave, F.E. Wilson, Reg. No. 2374, NMV. NEW SOUTH WALES: paratype ♀ of *S. irregularis*, Dorrigo, W. Heron, ANIC. Synonymy based on comparison of types.

Voucher specimens - VICTORIA: 1 ♀, 1 ♂, Matlock Ck, Mt. Gregory track, 10.*ii*.1977, A.A. Calder, NMV; 1 L, Thomson R., Thomson-Jordan Divide Rd, 1.*iii*.1978, NMV-SD, NMV.

Other material examined - VICTORIA: 5 ♀♀, 13 ♂♂, Matlock Ck, Mt. Gregory track, 10.*ii*.1977, A.A. Calder, NMV; 4 ♀♀, 2 ♂♂, Sassafras Ck, nr Monbulk, 19.*xi*.1972, PZ; 3 ♀♀, 10 ♂♂, Clematis Ck, nr Belgrave 19.*xi*.1972, PZ; 1 ♀ (with pupal and larval exuviae), Dandenong Ra, date? PZ; 2 ♀♀, Fern Tree Gully, 3.*i*.1911, Coll?, NMV; 1 ♀, 2 ♂♂, Acheron R., 4.*xi*.1972, PZ; 2 ♂♂, Chain Bay Ck, Mt. Buller, 20.*xii*.1972, PZ; 1 ♀, Eurobin Falls, Mt. Buffalo, 24.*xi*.1972, PZ; 1 ♀, Rubicon, 15.*xii*.1955, AN, NMV; 2 ♀♀, Taggerty, 15.*xii*.1956, AN, NMV; 1 ♂, Buxton, 15.*xi*.1967, AN, NMV; 1 ♂, Meredith, 12.*ii*.1959, AN, NMV; 2 ♂♂, Little R., nr Wulgulmerang, 14.*ii*.1969, AN, NMV; 1 ♀, 1 ♂, Noorinbee, 20.*xi*.1965, AN, NMV; 1 ♀, Kinglake, date?, F.E. Wilson, NMV; 1 ♀, 1 ♂, Warrandyte, 13.*i*.1976, AN, NMV; 2 ♀♀, Warbuton, Jan. 1926, F.E. Wilson, NMV; 1 ♂, Narracan, 15.*xi*.1969, AN, NMV; 1 ♀ (with pupal and larval exuviae) Traralgon Ck, 27.*i*.1979, A. Glaister, emerged in lab. 1.*vii*.1979; 1 ♂ (with pupal and larval exuviae) Flynns Ck, 23.*i*.1979, A. Glaister,

emerged in lab. 24.*iv*.1979; 1♀, 1♂ (with pupal and larval exuviae), Upper Pretty Valley, nr Mt. McKay, Bogong High Plains, 7.*i*.1973, PZ; 1♂ , Lock R., Noojee, 1.*xii*.1978, P. Suter, NMV-SD; 1♀ , Thomson R., Thomson Portal Rd, 10.*ii*.1977, NMV-SD; 1 ♂, Aberfeldy R., 10 km NNW Walhalla, 27.*xi*.1977, A.A. Calder, NMV; 30 L, Thomson R., various sites from Thomson Valley Rd to Aberfeldy Rd., 0.5 km downstream of Swingler Portal (Appendix A) 24.*xi*.1976-i.*iii*.1978, NMV-SD; 1 L, Thomson R., Moe-Walhalla Rd, 24.*x*.1977, NMV-SD; 17 L, Matlock Ck, Mt. Gregory track, 10.*ii*.1977-25.*xi*.1977, NMV-SD; 7 L, Matlock Ck, off Thomson Portal Rd, 24.*xi*.1976-10.*ii*.1977, NMV-SD; 3 L, Whitelaw Ck, at Whitelaw Portal, 11.*ii*.1977, NMV-SD; 2 L, Upper Macalister R., above Howitt Plain, 15.*xi*.1977, 22.*ii*.1977, NMV-SD; 15 L, Thomson-Jordan R. Jn, Divide Rd, 27.*xi*.1979-1.*vi*.1980, NMV-SD; 12 L, Traralgon Ck, 5.*v*.1979, NMV-SD; 3 L, Traralgon Ck on Traralgon Ck Rd, 27.*i*.1979, A. Glaister; 2 L, Traralgon Ck, Western Tyers Rd, 27.*i*.1979, A. Glaister; 1 L, Middle Ck, 5.*v*.1979, NMV-SD; 1 L, Little Morwell R, 5.*v*.1979, NMV-SD; 7 L, Western Tyers R., Christmas Ck Rd, 9.*v*.1979, NMV-SD; 10 L, Middle Tyers R. above Tyers Jn, 9.*v*.1979, NMV-SD; 1 L, Western Tanjil R. on Saxtons Rd, 10.*v*.1979, NMV-SD; 4 L, Latrobe R. at Hawthorn Ck, 10.*v*.1979, NMV-SD; 1 L, Same locality 1.*xii*.1978, P. Suter; 1 L, Latrobe R. on Powellton-Noojee Rd, 11.*v*.1979, NMV-SD; 1 L, Latrobe R., 9.8 km W Noojee, 17.*v*.1979, NMV-SD; 10 L, Loch R., 14.5 km N Noojee, 11.*v*.1979, NMV-SD; 15 L, Loch R. upstream of Icy Ck, 30.*xi*.1978, P. Suter; 6 L, Toorongo R. 1 km S Toorongo Rd, 12.*v*.1979, NMV-SD; 4 L, Pennyweight Ck, nr Noojee, 18.*ix*.1971, WDW; 2 L, Flynns Ck, on Lyndon Rd, 23.*i*.1979, A. Glaister; 2 L, Ferntree Gully, Melbourne; Aug. 1959, C. Watts; 5 L, Sassafras Ck, Sherbrooke, 20.*viii*.1978, A. Glaister; 1 L, Trib. Sassafras Ck, Sherbrooke, 16.*ix*.1978, A. Glaister; 2 L, Sassafras Ck on Old Patch Rd, 8.*ix*.1972, PZ; 36 L, Sassafras Ck, Dandenongs, Belgrave and Monbulk, 15-16.*ii*.1973, PZ; 14 L, Dandenong Rd., Melbourne, date?, PZ; 1 L, Dandenongs, Belgrave, Jun. 1972, PZ; 4 L, Yarra R. upstream of dam, 3.*xii*.1979, J. Smith;

CIT; 2 L, Yarra R. upstream Andersons Ck, 23.*x*.1979, J. Smith, CIT; 5 L, Home Ck, Glenewart Launching Place, 8.*vi*.1977, A. Glaister; 116 L, Running Ck, Kinglake National Park, April. 1977-July.1978, A. Fletcher; 100 + L, Monbulk Ck, nr Monbulk, 1961, 1962, 1963, 1964, 1968, WDW; 1 L, Monbulk Ck, Belgrave Picnic Ground, 27.*vi*.1971, WDW; 3 L, Delatite R. below sawmill settlement, 2.8 mi. below Mirmbah, 30.*vi*.1972, WDW; 113 L, Delatite R., 25.*ii*.1971-27.*xii*.1972, H.B.N. Hynes, PZ; 55 L, Godfreys Ck, 27.*i*.1971-24.*ix*.1972, H.B.N. Hynes, PZ; 95 L, Crown Ck, Woods Point, 24.*ii*.1971-28.*iv*.1972, H.B.N. Hynes, PZ; 4 L, Crown Ck, above Woods Point, 30.*vi*.1971, WDW; 1 L, Acheron R. at highway, 4.*ii*.1972, PZ; 1 L, Acheron R., 14.*vii*.1971, H.B.N. Hynes, PZ; 27 L, Acheron R., 23.*ii*.1975, L. Macmillan, PZ; 3 L, Trib. of Acheron R., on road, 14.*ii*. 1971, H.B.N. Hynes, PZ; 1 L, White Bridge, Mt. Buller Rd, 26.*vii*.1971, WDW; 27 L, White Bridge, Mt. Buller, 30.*vi*.1971-3.*x*.1972, H.B.N. Hynes, PZ; 25 L, Chalet Ck, White Bridge, Mt. Buller, 11.*v*.1972-2.*x*.1972, PZ; 15 L, Ck on Mt. Buller, date?, PZ; 1 L, Chain Bay Stream, on road by Chain Bay, 4.6 mi. above Mirmbah, 30.*vi*.1971, WDW; 2 L, Taponga R., 27.*ii*.1973, WDW; 4 L, Tawonga R., Bright, 16.*v*.1972, PZ; 1 L, Scrubby Ck, nr Mitta Mitta, Feb. 1962, WDW; 12 L, Creek under Mt. McKay, Pretty Valley, Bogong High Plains, 7.*i*.1973, PZ; 1 L, Bogong High Plains, nr Falls Creek, 12.*iv*.1972, PZ; 1 L, Howqua R., Mt. Timbertop-Mt. Macedon, date?, PZ; 2 L, Tanjil R., 24.*v*.1972, PZ; 1 L, West Tanjil R., July, 1972, PZ; 1 L, West Tanjil R., Mt. Baw Baw, 18.*xi*.1971, H.B.N. Hynes, PZ; 1 L, Cement Ck, 16.*ix*.1971, H.B.N. Hynes, PZ; 4 L, Myrtle Ck, Warburton, 30.*iv*.-4.*vi*.1972, PZ; 1 L, Weeping Rock, Warburton, 5.*v*.1972, PZ; 2 L, 5.2 mi. from summit of Mt. Donna Buang, 0.9 mi. from Cement Ck, 14.*vii*.1971, H.B.N. Hynes, PZ; 143 L, Wilks Ck, Marysville, 26.*ii*.1971-25.*x*.1972, H.B.N. Hynes, PZ; 1 L, Taggerty R. Marysville, 26.*iv*.1972, H.B.N. Hynes, PZ; 39 L, Bakers Ck, Jamieson, 12-28.*vi*.1972, H.B.N. Hynes, PZ; 4 L, Stevenson R., Buxton, 28.*xii*.1972, PZ; 2 L, Murrindindi R., nr Jamieson, 16.*v*.1978, J.A. Smith; 8 L, Stoney Ck, 16.*v*.1978, J.A.

Smith, 2 L, Grey R., Otway Ra., 20.*xii*.1978, H.B.N. Hynes; 1 L, Wild Dog Ck, Otway Ra., 19.*viii*.1972, PZ.

NEW SOUTH WALES: 1 ♀, Thredbo R., 4.*i*.1973, PZ; 1 ♀, Bourkes Ck, nr Captains Flat, 6.*xii*.1965, S. Allen, ANIC; 1 ♀, Windsor, date?, H.J. Carter, ANIC; 5 ♀♀, 1 ♂, Dorrigo, date?, W. Heron, ANIC; 1 ♀, 1 ♂, Dorrigo, date?, SAM; 1 ♂, Sydney, date?, Lea, SAM; 45 L, Pretty Valley Ck, Perisher Valley, 21.*i*.1979, J. Waterhouse; 3 L, Snowy R, nr Seamans Hut, Mt. Kosciusko, 19.*i*.1979, J. Waterhouse; 2 L, Caves Ck, Kosciusko National Park, 18.*vi*.1979, K. Bishop; 4 L, Snowy R, 8.*ii*.1966, E.F. Riek, ANIC; 9 L, Brown Mountain, 18.*i*.1961, E.F. Riek, ANIC; 1 L, Blue Lake, Mt. Kosciusko, 23.*xi*.1961, PZ; 11 L, Stream between Blue Lake and Hedley Tarn, Mt. Kosciusko, 3.*ii*.1976, PZ; 1 L, Dead Horse Gap, Mt. Kosciusko, 13.*iv*.1972, PZ; 1 L, Cabbage Tree Ck, Canberra-Coast Rd., 28.*vii*.1965, E.B. Britton, ANIC; AUSTRALIAN CAPITAL TERRITORY: 1 L, Blundells, 6.*i*.1961, E.F. Riek, ANIC.

Description

As given by Blackburn (1892) with the following additions based on an examination of voucher specimens; ♀,♂ and larvae.

Female (Figures 3.10-3.12)

Total length 4.9 mm, head width 0.9 mm, pronotal length 0.9 mm, pronotal width 2.7 mm, width between apical angles pronotum 0.45 mm, scutellar length 0.35 mm, scutellar width 0.45 mm, elytral length 3.9 mm, elytral width 3.25 mm.

General shape - Oval, convex.

Head - Black, dense ashen pubescence overall, antennal segments 1 and 2 yellow, remainder black.

Pronotum - Black with red patches at base, coarse white pubescence overall, sparser in medial region, lateral margins yellow, curving regularly from base to shallow apical angles.

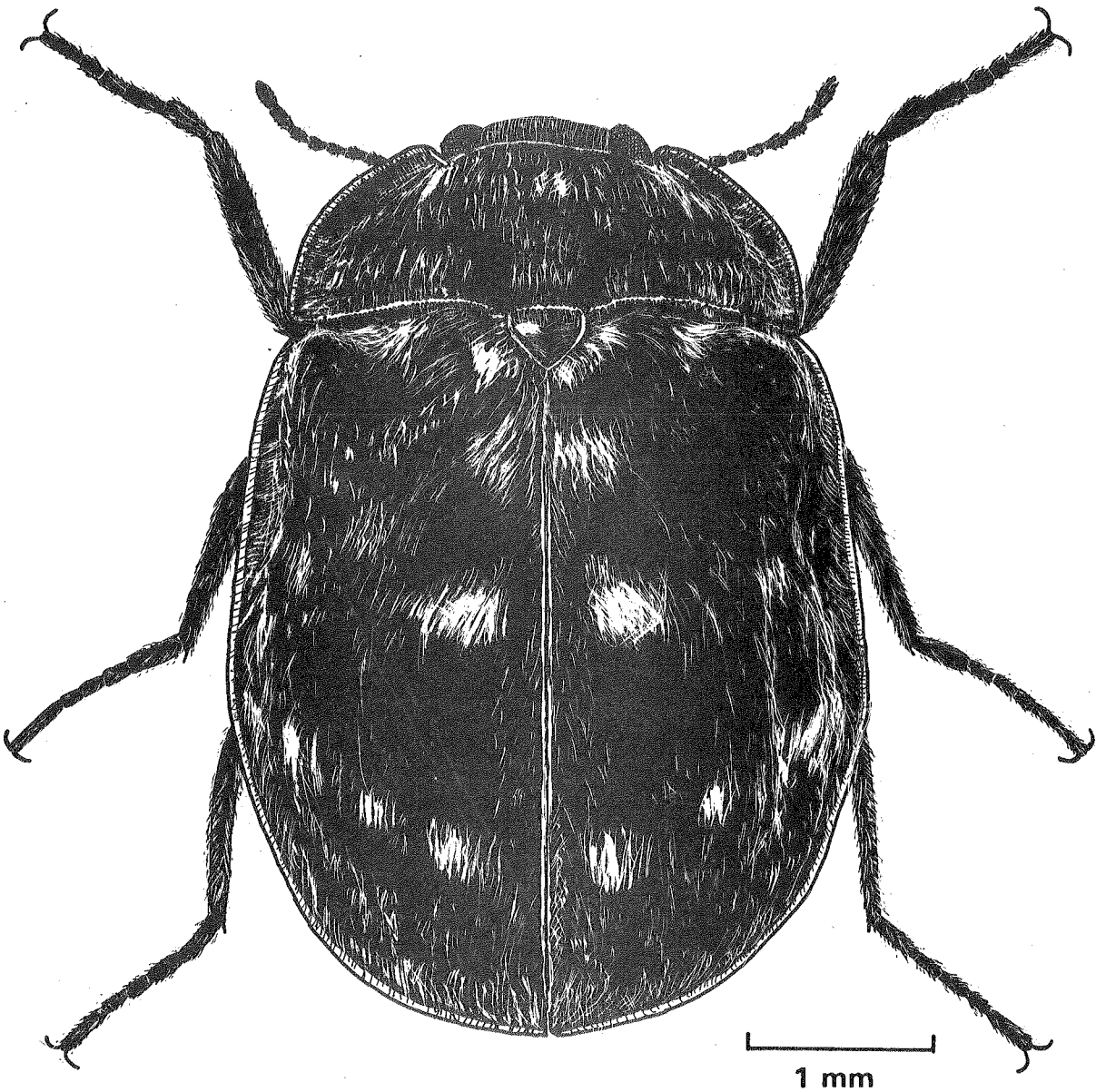


FIGURE 3.10 *Sclerocyphon maculatus*, ♀ voucher specimen, dorsal view. Scale line = 1 mm.

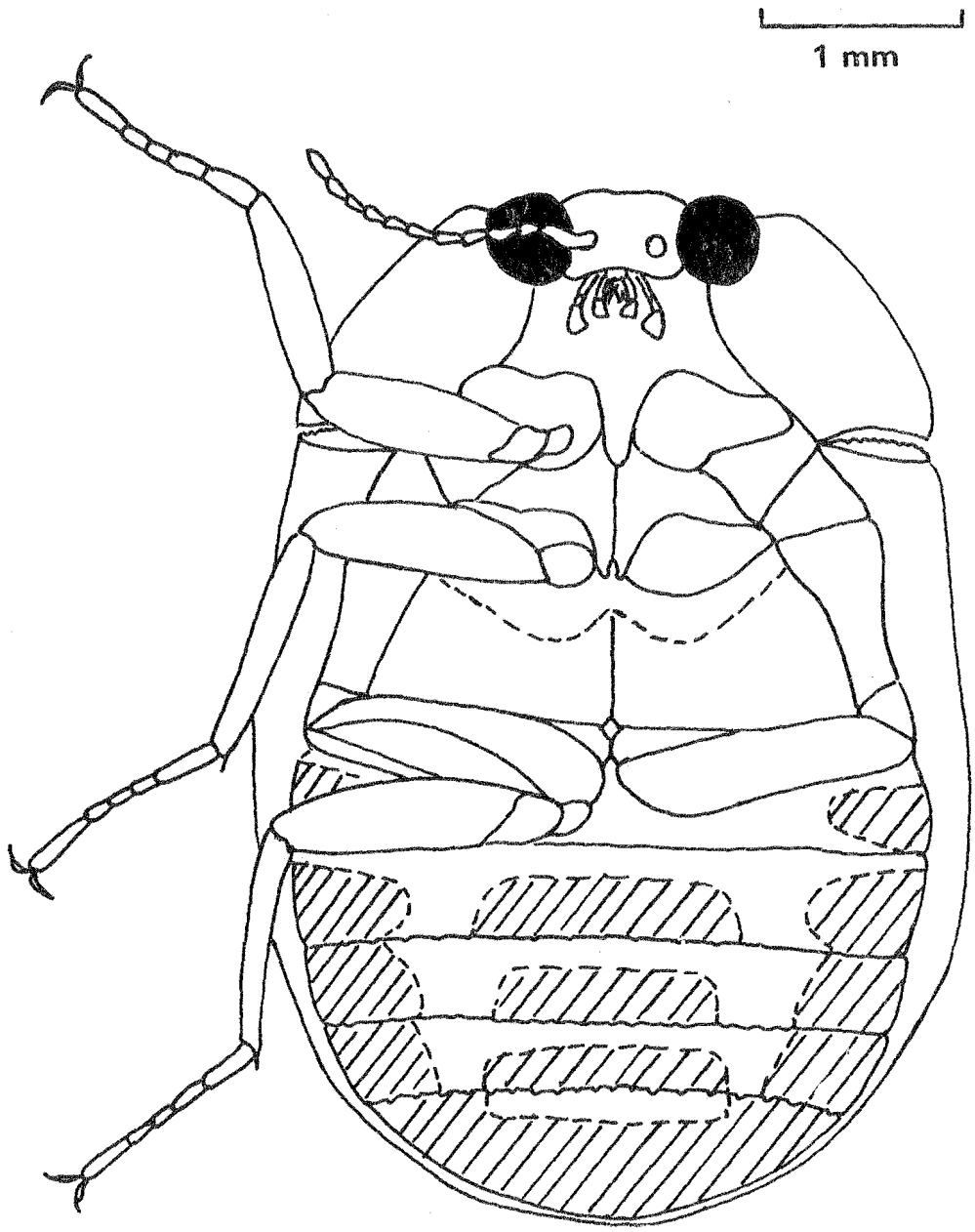
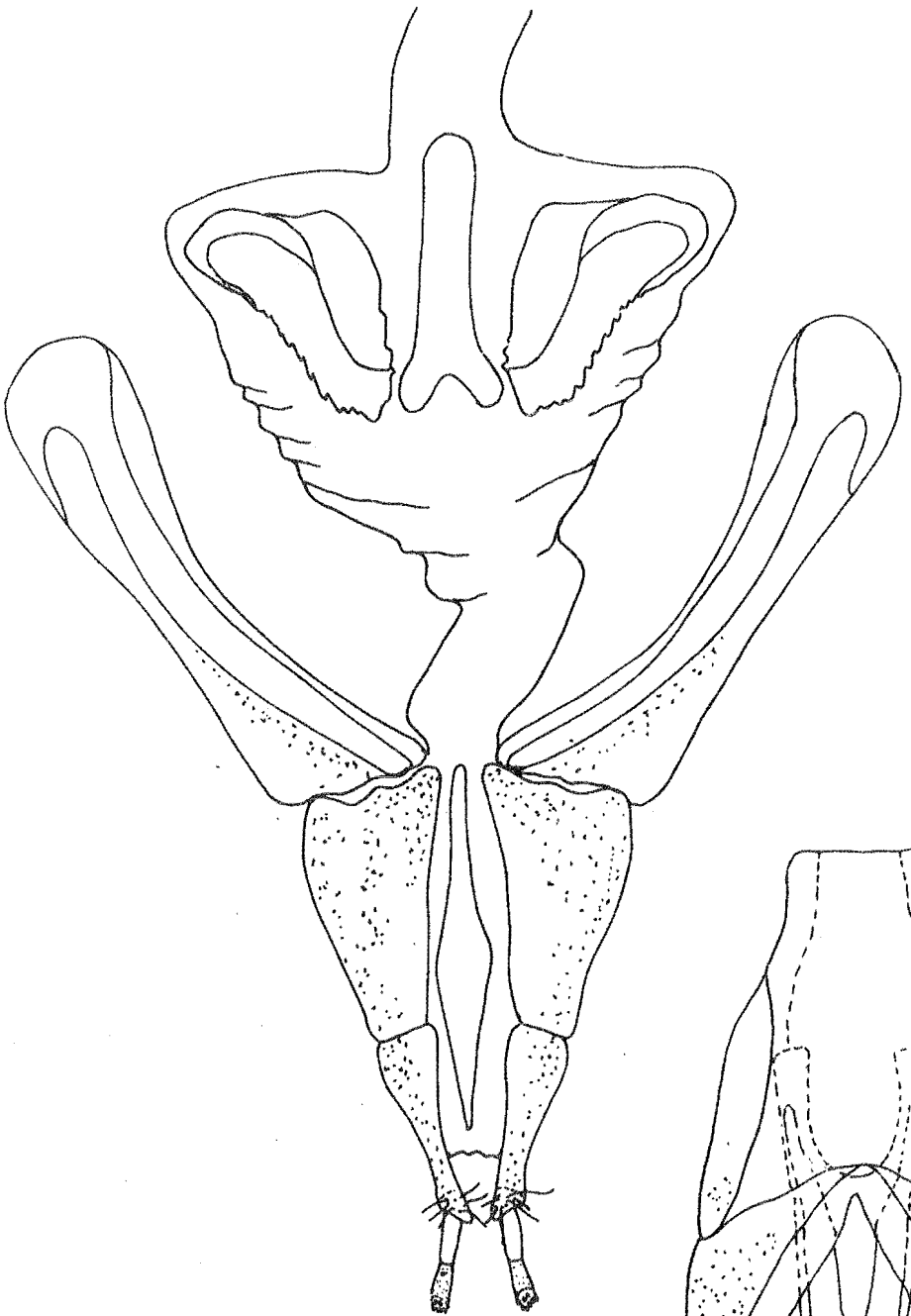


FIGURE 3.11 *Sclerocyphon maculatus*, ♀ voucher specimen, ventral view
Scale line = 1 mm.



FIGURES 3.12-3.13 *Sclerocyphon maculatus*: (3.12) ♀, external genitalia, ventral view; (3.13) ♂, external genitalia, ventral view. Scale line = 0.5 mm.

Scutellum - Black.

Elytra - Black with red-yellow patches, red-yellow at base and each side of elytral suture. Coarse white pubescence scattered overall, abraded in places exposing shining derm, dense patches of pubescence at medial third and two-thirds. Greatest width attained two-thirds from base, elytra gently swollen attaining greatest height at two-thirds, also. Margins narrow, yellow.

Legs - Femur black, tibia brown, tarsi yellow.

Thorax - Prosternum yellow, meso- and metasternum black with ante-coxal piece yellow. Mesoepisternum yellow.

Abdomen (Figure 3.11) - Segments 1-4 black laterally and medially, elsewhere red-yellow. Segment 5 black with medial region yellow.

External genitalia (Figure 3.12) - Pair of sclerotised hemisternites punctate, setose distally, bearing 2-segmented styli, proximal segment membranous, distal segment sclerotised but with membranous tip bearing minute apical projections. Sclerotised rod, expanded medially, embedded in vaginal wall between hemisternites. Pair of sclerotised plates embedded in anterior dorso-lateral vaginal walls, triangular and widened at base.

Male (Figure 3.13)

Total length 4.15 mm, head width 0.85 mm, pronotal length 0.8 mm, pronotal width 2.3 mm, width between apical angles of pronotum 1.0 mm, scutellar length 0.3 mm, scutellar width 0.35 mm, elytral length 3.3 mm, elytral width 2.7 mm.

Similar to female but smaller.

External genitalia (Figure 3.13) - Aedeagus symmetrical, trilobate, parameres sclerotised, punctate, narrowing to membranous tips. Penis complex, consisting of two sclerites, dorsal sclerite with lateral margins sloping to narrow apex, ventral sclerite smaller with rounded apex.

Last instar larva (Figure 3.14, Pls 3.2-3.4)

Total length 7.1 mm, total width 3.7 mm, length of ninth tergite 1.1 mm, width of ninth tergite 1.6 mm.

General shape - Narrow elongate thoraco-abdominal shield, widest at metanotum, tapering to tergite 9.

Dorsal surface - Medial region with 3 dark brown-black bands, one band on thorax, one on adjoining tergites 3, 4, 5 and one on tergite 8. Remainder of medial region yellow, pronotum with yellow patch medially and above each eye. Lateral laminae lighter brown with yellow patch medially. Tergite 9 dark with 3 lighter patches at posterior margin.

Entire marginal fringe of setae with two bands visible; a narrow, regular, stiff, inner section, and a wider transparent outer section where setae soft, flexible, tapering to a minute point. Trailing edge of all laminae with fringe of fine transparent setae.

Dense uniform covering of sclerotised cuticular beads smaller but denser in medial region, larger but sparser on laminae, dense dark clump of beads at junction of lamina and body on tergites 1-8.

Many pores visible, covered with shining mucus, in medial region of pro-, meso- and metanotum, also extending across tergites 1-8, densest on upraised region each side of ecdysial scar, on each side of sagittal line.

Twelve paired groups of trichoid sensilla in medial region, one group to each side of midline on each thoracic and abdominal segment. Discrete sensilla visible only with scanning electron microscopy. Under light microscopy clumps pale and shining due to the presence of muco-polysaccaride secretions. Each pair, on an upraised region, often forming an inverted "Y" around midline, most distinct on tergites 3-7, poorly developed on pro-, meso- and metanotum.

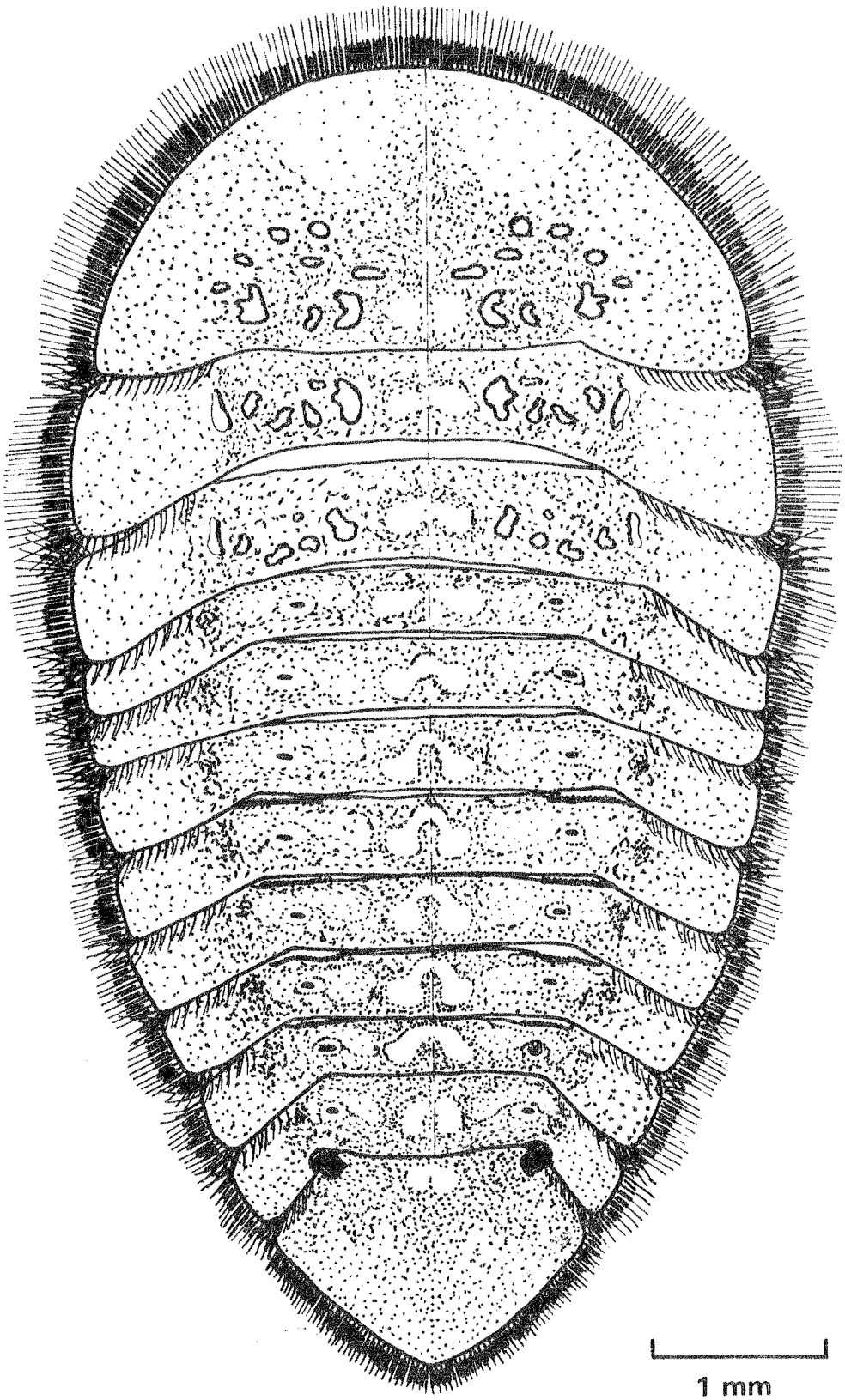
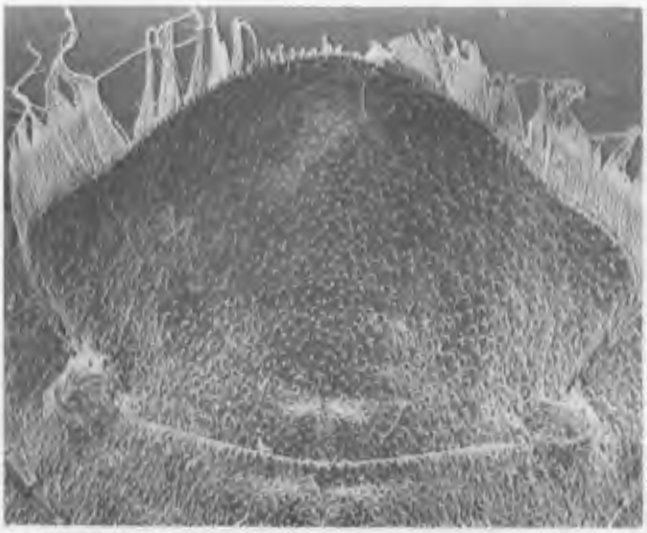
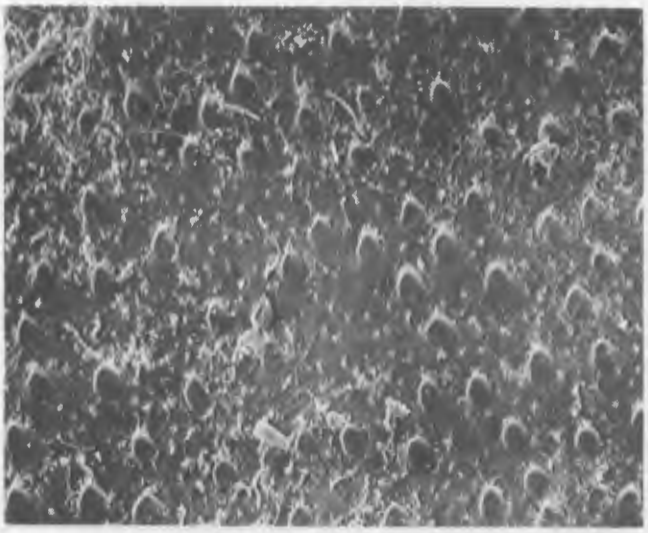


FIGURE 3.14 *Sclerocyphon maculatus*, last instar larva, voucher specimen, dorsal view. Scale line = 1 mm.

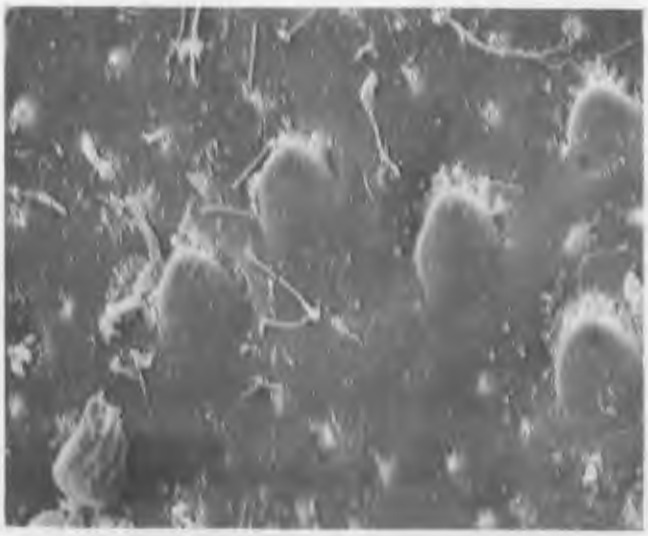
3.2



3.3



3.4



Plates 3.2-3.4 *Sclerocyphon maculatus*, last instar larva from Matlock Ck, tergite 9: (3.2) x 40; (3.3) x 200; (3.4) x 650.

Pronotum with 5 pairs of irregularly shaped pits and 4 pairs of circular pits. Meso- and metanotum with 6 pairs of irregular pits. All pits yellow, bordered by cuticular beads.

Four pairs of gin traps present on adjoining margins of tergites 3-4, 4-5, 5-6 and 6-7. Three anterior pairs of similar width, fourth pair narrower. Only the lower margin of each gin trap thickly sclerotised giving the appearance of 4 "half" gin traps.

Tergite 9 (Pls 3.2-3.4) with sloping lateral margins and triangularly curved posterior margin. No ridges present, anterior medial region slightly raised, sloping to lateral and posterior margins. Dense covering of cuticular beads over entire tergite, slightly sparser posteriorly.

Diagnosis

Adults can be distinguished by the following combinations of characters; relatively small size, convex body, elytra swollen in apical third, alternating regions of coarse white pubescence and glabrous shining derm dorsally, and narrow tapered penile sclerites or anteriorly widened, triangular vaginal plates.

Larvae can be distinguished by the following combination of characters; 4 "half" gin traps, tergite 9 lacking ridges and with posterior margin triangularly curved, and the distinctive inverted "Y" form of the clumps of trichoid sensilla .

Comments

Blackburn's (1895) description of one specimen was not considered adequate, in the light of present knowledge, and these additional descriptions are given based on an examination of male and female voucher specimens.

Adult and larva were first linked by Bertrand and Watts (1964), adults have also been reared from larvae in the laboratory in this study. A re-description of the larva is also given to facilitate comparison with larvae of other *Sclerocyphon* described below.

Carter (1935) stated that *S. maculatus* was widespread in Queensland, New South Wales, Victoria and Tasmania. While present records indicate that this species is fairly abundant and widespread in eastern Victoria and southern New South Wales its occurrence in either Queensland or Tasmania is highly unlikely. *S. maculatus* could easily have been confused with several other morphologically similar species. The specific epithet, although accurate, is not diagnostic as several other species also exhibit the dark/light colour pattern. Much of Blackburn's description must now be regarded as applicable to the entire genus rather than *S. maculatus* alone.

S. maculatus larvae represent a very distinct form within *Sclerocyphon*, the 4 "half" gin traps and upraised, inverted "Y"-shaped clumps of mucus-coated sensilla are unique to this species. Variation in larval form is also evident with some larval populations exhibiting a much broader, larger, thoraco-abdominal shield. This broader shield has been noted most often in specimens from cooler alpine localities although not exclusively so. The beetle described by Carter (1935) as *S. irregularis* (preserved on card with its larval and pupal exuviae) had emerged from a larva of wide body form. Comparison of this beetle with the *S. maculatus* type revealed that they are, in fact, conspecific.

Sclerocyphon striatus Lea

(Figures 3.15-3.19, Pls 3.5-3.9)

Sclerocyphon striatus Lea, 1895, p.597

Material Examined

Types - NEW SOUTH WALES: holotype ♀, Tamworth, SAM. Paratype ♀ and ♂, Tamworth, SAM.

Voucher specimens - VICTORIA: 1 ♀, Thomson R., Bells Clearing, 6 km S Aberfeldy, MV light, 9.*ii*.1977, A.A. Calder, NMV; 1 ♂, same locality, MV light, 11.*ii*.1977, A.A. Calder, NMV; 10 L, Swamp Ck, Kiewa Hwy, 18.*v*.1979, J.A. Smith, NMV.

Other material examined - VICTORIA: 16 ♀♀, 14 ♂♂, (8-11.*ii*.1977), 1♀, 1♂ (9.*ii*.1977), 1 ♀(25.*ii*.1977), 4♀♀, 2♂♂ (2.*xii*.1977), 2♀♀, 1♂ (25.*ii*.1978) all Thomson R., Bells Clearing, MV light, NMV-SD; 14♀♀, 11♂♂ (16.*ii*.1977) 49 L (4.*xii*.1976-24.*ii*.1978) all Macalister-Caledonia R. jn, NMV-SD; 12 ♀♀, 6 ♂♂ (6.*xii*.1977), 35 L (5.*v*.1977-24.*ii*.1978) all Macalister-Barkly R. jn, MV light, 6.*xii*.1977, NMV-SD; 8 ♀♀, 6 ♂♂, Wellington-Carey R. jn, 15.*ii*.1977, A.A. Calder, NMV-SD; 1 ♀(1.*xii*.1976), 3 ♀♀, 5 ♂♂ (23.*ii*.1978), 18 L (1.*xii*.1976-23.*ii*.1976), all Macalister-Wellington R. jn, MV light, A.A. Calder, NMV-SD; 1 ♀, Macalister R., 6 km NNW Glenmaggie, 4.*xii*.1976, A.A. Calder, NMV-SD; 5 ♀♀, 10 ♂♂, Wellington R., 17 km N of Licola, 14.*ii*.1977, MV light, NMV-SD; 1 ♀, 6♂♂ (25.*ii*.1978), 3 L (24.*ii*.1978) all Wellington R., 23.5 km NNE Licola on Tamboritha Rd, MV light, NMV-SD; 1 ♀, Pe*, Le**, Mitta Mitta R., 28.*x*.1978, A. Glaister, emerged in lab. 20.*xi*.1978; 1 ♂, Pe, Le, Mitta Mitta R., 15.5 km NW Benambra, 31.*x*.1978, A. Glaister, emerged in lab. 28.*xi*.1978; 2 ♂♂, Pe, Le, Mitta Mitta R., 29.*x*.1978, A. Glaister, emerged in lab. 13-14.*xi*.1978; 1 ♂, Pe, Le, Mitta Mitta R., 19.*ii*.1979, A. Glaister, emerged in lab. 26.*vii*.1979; 1 ♀, Pe, Le, Mitta Mitta R., 21.*ii*.1979,

* Pe = pupal exuvium; ** Le = larval exuvium

A. Glaister, emerged in lab. 1.*vii*.1979; 2 ♂♂, Pe, Le, Deep Ck, nr Bulla, *x*.1978, A. Glaister, emerged in lab. Dec.1978, 2 ♀♀, Pe, Le, Deep Ck, nr Bulla, 18.*xii*.1978, A. Glaister, emerged in lab. 3.*i*.1979; 1 ♀, Pe, Le, Deep Ck, nr Bulla, 18.*xii*.1978, A. Glaister, emerged in lab. 1.*vii*.1979; 1 ♀, Pe, Le, Traralgon Ck, 27-29.*i*.1978, A. Glaister, emerged in lab. 3.*xi*.1979; 1 ♀, 2 ♂, Pe, Le, Ovens R., Harrietville, 23-28.*xi*.1972, PZ; 4♀♀, Pe, Le, 8-21.*x*.1972, 3 L, 17.*ii*.1972, Bostock Ck, nr Colac, PZ; 1 ♀, Pe, Le, 3 L, Steels Ck, nr Yarra Glen, date?, PZ; 1♂ (+ Pe + Le), Flourbag Ck, on road from Jamieson to AI Mine Settlement, 17.*x*.1972, PZ; 1 ♂, Crown Ck, nr Woods Point, 28.*xii*.1971, PZ; 2♀♀, 2♂♂, Pe, Le, 18 L, Upper Pretty Valley, Bogong High Plains, date?, PZ; 8 L, Bogong High Plains, nr Falls Ck, 12.*iv*.1972, PZ; 3 L, Pretty Valley Pond, Pretty Valley, under Mt. McKay, Bogong High Plains, 7.*i*.1973, PZ; 14 L, Upper Pretty Valley, Falls Ck, 7.*i*.1975, PZ; 1 ♀, 7 L, Carisbrook Ck, Otway Ra., 20.*xii*.1978, H.B.N. Hynes; 2 ♀♀, 2 ♂♂, Tambo Crossing, 24.*i*.1960, A. Neboiss, NMV; 1 ♂, Licola, 15.*ii*.1965, A. Neboiss, NMV; 1 ♀, Sassafras Gap, 13.*ii*.1963, A. Neboiss, NMV; 1 ♂, Little R., 3 km SE Taggerty, 6.*i*.1972, A. Neboiss, NMV; 1 ♀, Dondangadale, 11.*i*.1955, A. Neboiss, NMV; 1 ♂, Avenel 9.*xii*.1954, A. Neboiss, NMV; 1 ♀, 4 ♂♂, Abbeyard, 27.*i*.1960, A. Neboiss, NMV; 2 ♀♀, Seven Creeks, 10 km SW Strathbogie, A. Neboiss, NMV; 1 ♀, 1♂, Thomson R., Knappings Clearing, 9.*iii*.1979, A. Neboiss, NMV; 3 ♀♀, 1 ♂, 4 km SW Healesville, 21.*ii*.1976, A. Neboiss, NMV; 20 ♀♀, 28 ♂♂, River Crossing, 10 mi. N Valencia Ck, via Maffra, 14.*i*.1966, MV light, B. Cantrell, T Weir, QU; 9 ♀♀, 4 ♂♂, The Gorge, Beechworth, 12.*i*.1967, B. Cantrell, QU; 1 ♂, Cann River, 28.*i*.1967, G. Monteith, QU; 232 L, Thomson R. sites (Appendix A) 22.*xi*.1979-2.*vi*.1980, NMV-SD; 115 L, Thomson R. sites (Appendix A) 24.*xi*.1976-3.*iii*.1978, NMV-SD; 9 L, Aberfeldy R. sites (Appendix A) 29.*xi*.1976-16.*viii*.1977, NMV-SD; 3 L, Whitelaw Ck, at Whitelaw Portal, 11.*ii*.1977-2.*vi*.1977, NMV-SD; 15 L, Rainbow Ck, Cowarr-Seaton Rd, 18.*ii*.1977, NMV-SD; 1 L, Dingo Ck, Caledonia R.

track, 30.*xi*.1976, NMV-SD; 24 L, Macalister R. sites (Appendix A) 4.*xii*.1976-23.*ii*.1978, NMV-SD; 2 L, Hellfire Ck, 22.*ii*.1978, NMV-SD; 12 L, Dolobrook R., Brandy Pinchmine, 2.*xii*.1976, NMV-SD; 58 L, Mitta Mitta R. sites (Appendix A) 2.*ii*.1975-28.*x*.1978, NMV-SD; 8 L, (7.*iii*.1977), 2 L (10.*ii*.1978) all Snowy Ck, NMV-SD; 2 L, Traralgon Ck, 5.*v*.1979, NMV-SD; 3 L, Middle Ck, 5.*v*.1979, NMV-SD; 1 L, Tyers R. on Yallourn-North Tyers Rd, 6.*v*.1979, NMV-SD; 1 L, Tyers R. at Walhalla Rd. bridge, 17.*v*.1979, NMV-SD; 3 L, Eastern Tanjil R. at Tanjil Jn, 8.*v*.1979, NMV-SD; 1 L, Middle Tyers R. above Tyers Jn., 9.*v*.1979, NMV-SD; 5 L (1.*xii*.1978) 4 L (10.*v*.1979) all Latrobe R. at Hawthorn Ck, NMV-SD; 2 L, Little Morwell R., 6.*v*.1979, NMV-SD; 1 L, Levens Ck, -*ii*.1961, WDW; 15 L, Little Scrubby Ck nr Mitta Mitta, -*ii*.1961, WDW; 3 L, Scrubby Ck nr Mitta Mitta, -*ii*.1962, WDW; 2 L, Big Snowy Ck, -*ii*.1972, WDW; 2 L, Ovens R. at Harrietville on Alpine Rd, 23.*iv*.1962, WDW; 3 L, Howqua R. where crossed upland by Howqua Trail, nr Mt. Timbertop and Mt. Macedon, 28.*ii*.1969, WDW; 1 L, Howqua R. 28.*ii*.1971, WDW; 4 L, Howqua R. stockyard, 15.*iv*.1972, PZ; 7 L (28.*iv*.1972), 4 L (25.*viii*.1972) all Flourbag Ck, Jamieson, H.B.N. Hynes, PZ; 1 L, Fryers Ck, Lake Eildon, 30.*vii*.1972, H.B.N. Hynes, PZ; 30+ L, Aberfeldy R. 24.*ix*.1971-26.*v*.1972, H.B.N. Hynes, PZ; 4 L, Stevenson R., Buxton, 28.*xii*.1972, PZ; 10 L, Acheron R., 23.*ii*.1975, L. McMillan, PZ; 1 L, Delatite R., 23.*ii*.1971, H.B.N. Hynes, PZ; 1 L, Taponga R., 22.*xi*.1971, H.B.N. Hynes, PZ; 1 L, Stringer Ck, below Walhalla, 29.*vi*.1971, H.B.N. Hynes, PZ; 1 L, King R., Whitfield, 12.*iv*.1972, PZ; 7 L (28.*iv*.1972), 4 L (25.*viii*.1972) all Flourbag Ck, Jamieson, H.B.N. Hynes, PZ; 8 L, Ovens R., East branch, 23.*ii*.1972, PZ; 29L, Swamp Ck, on Kiewa Hwy, 18.*v*.1979, J.A. Smith; 2 L, Still Ck on Eildon-Jamieson Hwy, 17.*v*.1979, J.A. Smith; 3 L, Snobs Ck at Falls, nr Alexandra, 17.*v*.1979, J.A. Smith; 1 L, Sevens Ck, 10 km SW Strathbogie, 26.*ix*.1978, A. Glaister; 18 L (May 1977), 56 L (July 1977), 75 L

(Oct. 1977), 72 L (Jan. 1978) all Watchbox Ck, Euroa, A. Fletcher; 5 L, Watchbox Ck, above falls, 10.*v*.1977, A. Fletcher; 5 L, Watchbox Ck, below falls, 8.*v*.1977, A. Fletcher; 62 L (April.1977), 2 L (April. 1977), 38 L (Oct.1977), 46 L (Jan.1978) all Running Ck, Kinglake National Park, A. Fletcher; 5 L, Running Ck, Mason Falls, Kinglake National Park, 16.*v*.1979, J.A. Smith; 8 L, Dry Ck, nr Stills Ck, 5 mi. N Yarra Glen, 29.*ix*.1972, PZ; 3 L, Watts R., upstream of Yarra R., 27.*xi*.1979, J. Smith, CIT; 4 L, Big Pats Ck, Yarra R., 23.*x*.1979, J. Smith, CIT: 2 L, Yarra R. upstream Big Pats Ck, 23.*x*.1979, J. Smith, CIT; 2 L, Yarra R. at Milgrove, 29.*x*.1979, J. Smith, CIT; 4 L, Yarra R. at Woori Yallock, 5.*xi*.1979, J. Smith, CIT; 1 L, Yarra R. upstream of Andersons Ck, 23.*x*.1979, CIT; 2+ L Plenty R. Mernda, 16.*xi*.1979, J. Smith, CIT; 1 L, Diamond Ck, Broughton Rd, 18.*xi*.1971, J. Smith, CIT; 2 L, Yarra R. 3 km SW McMahons Ck, 16.*xi*.1976, A. Wells, WDW; 4 L, Maribyrnong R., Sydenham Park, 1980, V. Brown, MMBW; 4 L, Andersons Ck, Everard Drive, 12.*iv*.1979, J. Dean, MMVW; 5 L, Andersons Ck, 16.*viii*.1979, J. Dean, MMBW; 1 L (Nov.1971), 1 L (Jan.1971) all Dandenong Ck, I. Campbell, PZ; 4 L, Creek on Bonang Hwy, 20 mi. N Orbost, 20.*ii*.1972, PZ; 2 L, Tambo R. Grayling Survey, in gut, 1979, T. Berra, P.D. Jackson; 1 L, Trib. of Wild Dog R., S of Warragul, 7.*viii*.1979, H.B.N. Hynes, PZ; 3 L, Eumarella Ck on Princes Hwy, 24.*xi*.1977, P. Suter, WDW; 1 L, Fitzroy R. at Tyrendarra, 24.*xi*.1977, P. Suter, WDW; 5 L, William Hall Ck, 21.*xi*.1976, J.E. Bishop, WDW; 2 L, Fyans Ck, Grampians, 29.*x*.1977, P. Suter, WDW; 2 L, Wennicott Ck on Casterton-Hamilton Rd, 19.*xi*.1977, P. Suter, WDW; 1 L, Bovine Ck, Grampians, 30.*x*.1977, P. Suter, A. Wells, WDW; 2 L, Flat Rock Crossing, 20 km W Halls Gap, 22.*ix*.1976, J.E. Bishop, WDW; 8 L, Jamieson R., Otway Ra., 19.*viii*.1972, PZ; 158 L, Barwon R., East branch, at outflow from Lake Elizabeth, 4.*iv*.1975-15.*vi*.1975, L. McMillan, PZ; 3 L, Apollo Bay, Jan. 1959, CW; 6 L, Deans Marsh, Jan. 1959, CW; 21 L, McKenzie Ck,

23.*i*.1976-15.*xii*.1977, P.D. Jackson, Fisheries and Wildlife, Victoria; AUSTRALIAN CAPITAL TERRITORY: 1 ♀, Paddys R., 31.*i*.1967, S. Muko, ANIC; 1 ♀, (7.*ii*.1967), 2 Pe, 3 L (3.*i*.1967) E.B. Britton, ANIC; 4 L, Paddys R. 6 mi. from Cotter, 15.*xi*.1964, E.B. Britton, ANIC; 5 L, Paddys R. Jan. 1964, H.E. Hinton, CW; NEW SOUTH WALES: 2 ♀, Dorrigo, date?, W. Heron, ANIC; 2 ♂♂, South Arm via Bowraville, 20.*i*.1966, B. Cantrell, QU; 2 ♀♀, Matheson, 1-5.*ii*.1964, J.C. Cardale, QU; 1 ♂, 28 L, Pages R., Murrurindi, 26.*i*.1980, J.A. Smith, emerged in lab. 3.*iii*.1980; 4 ♀, 2 ♂, 24 L, Peel R. Nundle, nr Tamworth, 26.*i*.1980, J.A. Smith, emerged in lab. March 1980; 1 L, Peel R., 1 km upstream from Nundle, 30.*iv*.1981, P.S. Lake, D. Coleman; 13 L, Gyra R. below Blue Hole weir, 14 km SE Armidale, 24.*iii*.1980, M.K. Notestine; 4 L, Barrington, 30.*viii*.1931, F.J. Gay, ANIC; 5 L, Creek E of Nundle, nr Tamworth, 27.*i*.1980, J.A. Smith; 2 L, Hunters R. Mooran Flat, 27.*viii*. 1978, H.B.N. Hynes; 1 L, Isis R. on road to Waverley, 26.*viii*.1978, H.B.N. Hynes; 2 L, Ex platypus cheek pouches, Upper Shoalhaven R., 11.*viii*.1977, R. Farragher; 3 L, Shoalhaven R., 12.*x*.1977, R. Farragher; 5 L, Gerrabattgull Ck, -*ii*.1979, R. Farragher; 9 L, Mongarlowe R., Trib. of Upper Shoalhaven R., 12.*i*.1976, K. Bishop; 18 L, Trib. of Tuross R., W of Narooma, 17.*i*.1980, J.A. Smith; 8 L, Gulph Ck, Neriggundah, 17.*i*.1980, J.A. Smith; 2 L, Endrick Ck, Nerriga, 18.*i*.1980, J.A. Smith; 17 L, Jaspers Ck, Princes Hwy, Nowra, 19.*i*.1980, J.A. Smith; 15 L, Snowy R. nr Seamans Hut, Mt. Kosciusko, 19.*i*.1979, J. Waterhouse; 4 L, Snowy R, 8.*ii*.1966, E.F. Riek, ANIC; 3 L, Caves Ck, Kosciusko National Park, 18.*vi*.1979, K. Bishop; 1 L, Small creek nr Dead Horse Gap, Mt. Kosciusko, date?, I. Campbell, PZ; 5 L, Jacobs R. 5 km S of Jindabyne, 2.*i*.1976, J.E. Bishop, WDW; 11 L, Macquarie R. at bottom of pass, 15.*ix*.1976, J.E. Bishop, WDW; 4 L, Geehi R., 7.*i*.1973, PZ; 2 L, Cooma, Jan.1961, CW; 4 L, Kowmung, Mar.1933, C. Davis, ANIC.

Description

As given by Lea (1895) but with the following additions based on an examination of voucher specimens; ♀, ♂ and larvae.

Female (Figures 3.15-3.17)

Total length 5.25 mm, head width 0.95 mm, pronotal length 0.95 mm, pronotal width 2.7 mm, width between apical angles of pronotum 1.25 mm, scutellar length 0.35 mm, scutellar width 0.45 mm, elytral length 4.25 mm, elytral width 3.25 mm.

General shape - Elliptic-elongate, subconvex beetle.

Head - Black, fine dense pubescence overall, antennal segments 1 and 2 yellow, remainder dark brown.

Pronotum - Dark brown with orange patches, covered overall with fine dense ashen pubescence. Medial region convex, medial line faintly visible, lateral margins flat, yellow.

Scutellum - Yellow.

Elytra - Dark brown with scattered orange/yellow patches, medial region lighter, very fine, dense ashen pubescence overall plus many small clumps of thicker, coarse, white pubescence. Glabrous brown patch on each side of suture at middle, bordered anteriorly by region of dense white pubescence, dense region of white pubescence extending in arc from suture to lateral margin at apical third. Striations faintly visible apically and laterally. Greatest width attained at apical third. Margins narrow, yellow.

Legs - Femur dark brown, tibia and tarsi yellow.

Thorax - Pro- and mesosternum and antecoxal piece yellow, remainder dark brown.

Abdomen (Figure 3.16) - Segments 1-5 black with lighter, orange patches.

External genitalia (Figure 3.17) - Pair of sclerotised hemisternites,

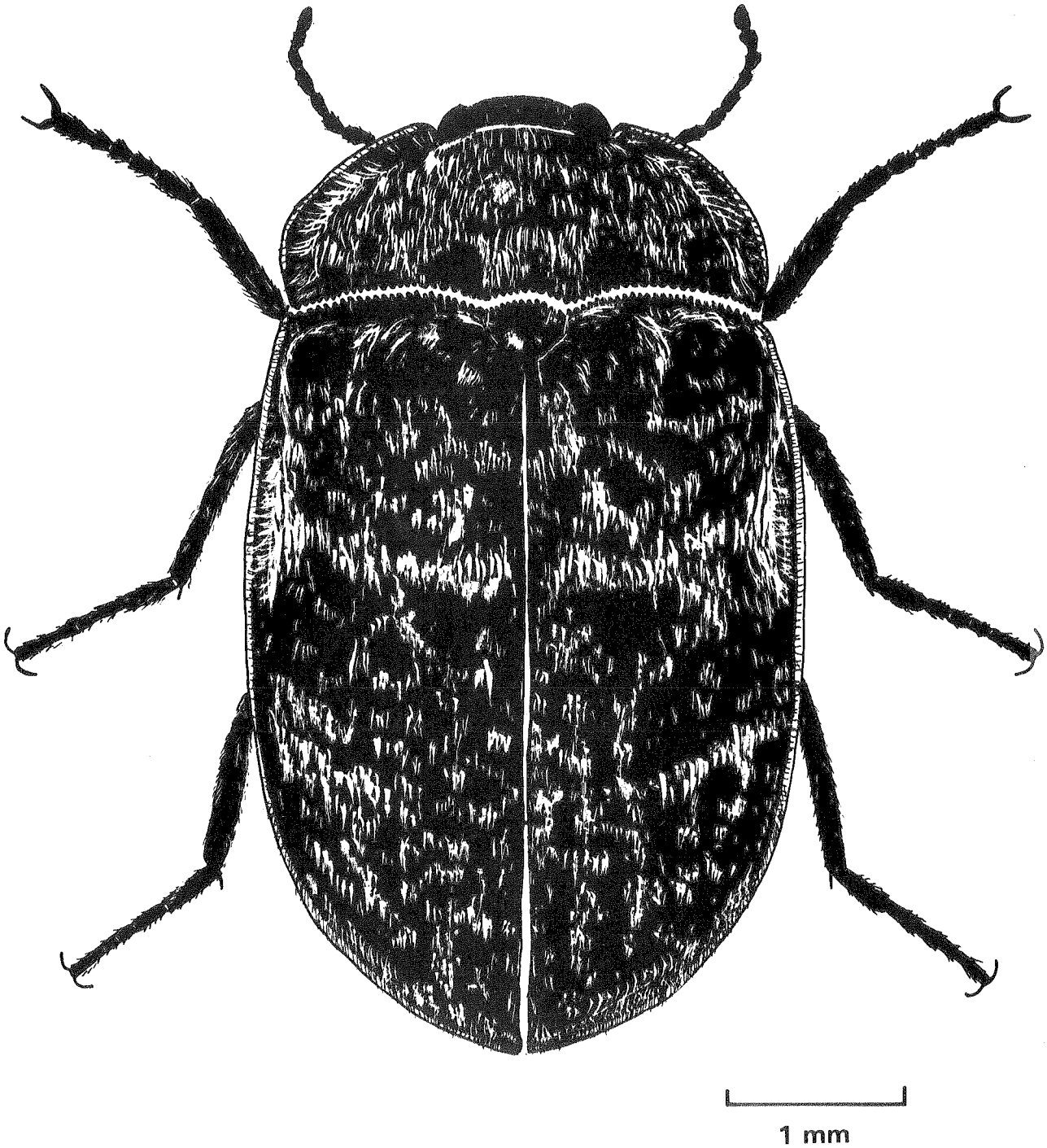


FIGURE 3.15 *Sclerocyphon striatus*, ♀ voucher specimen, dorsal view. Scale line = 1 mm.

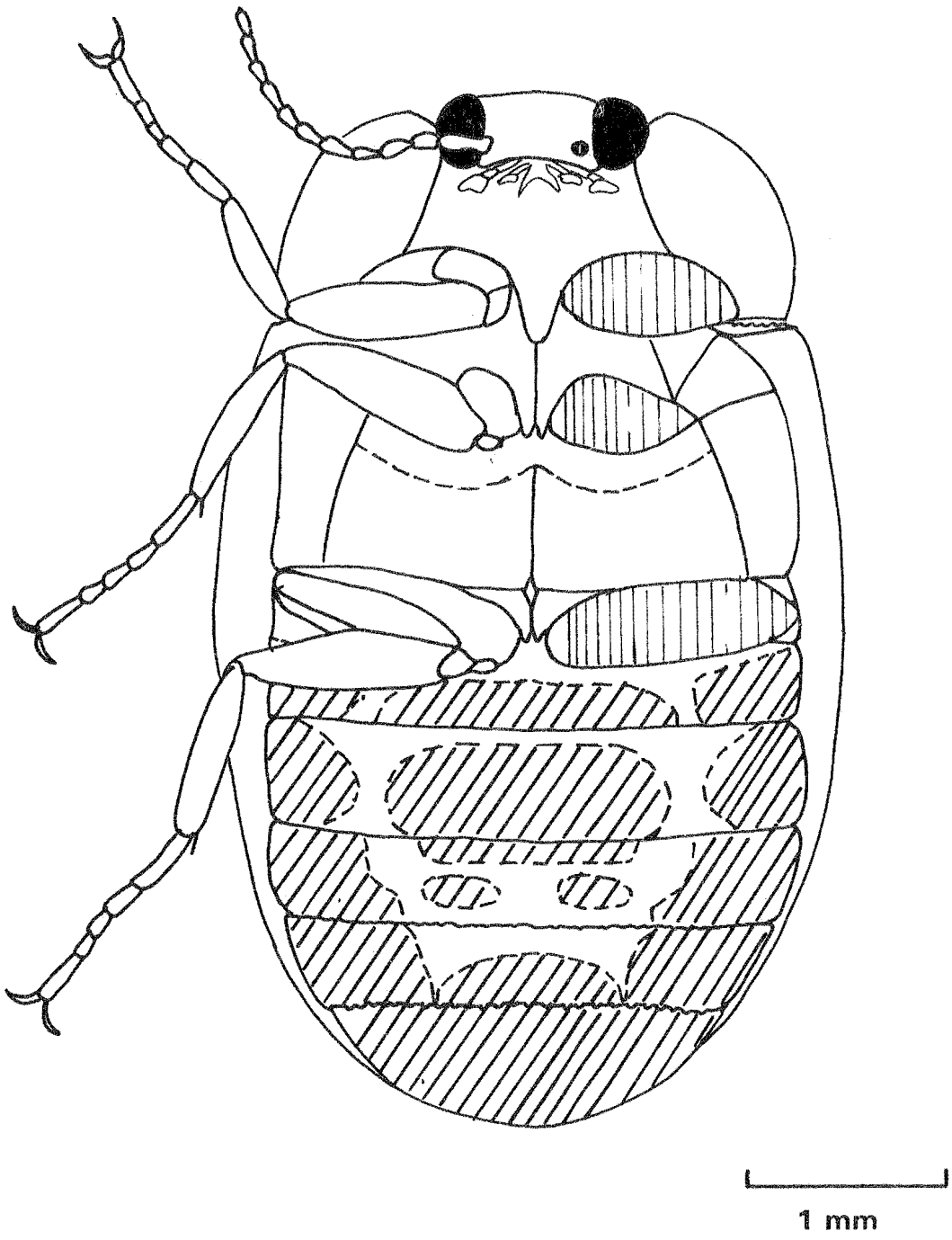
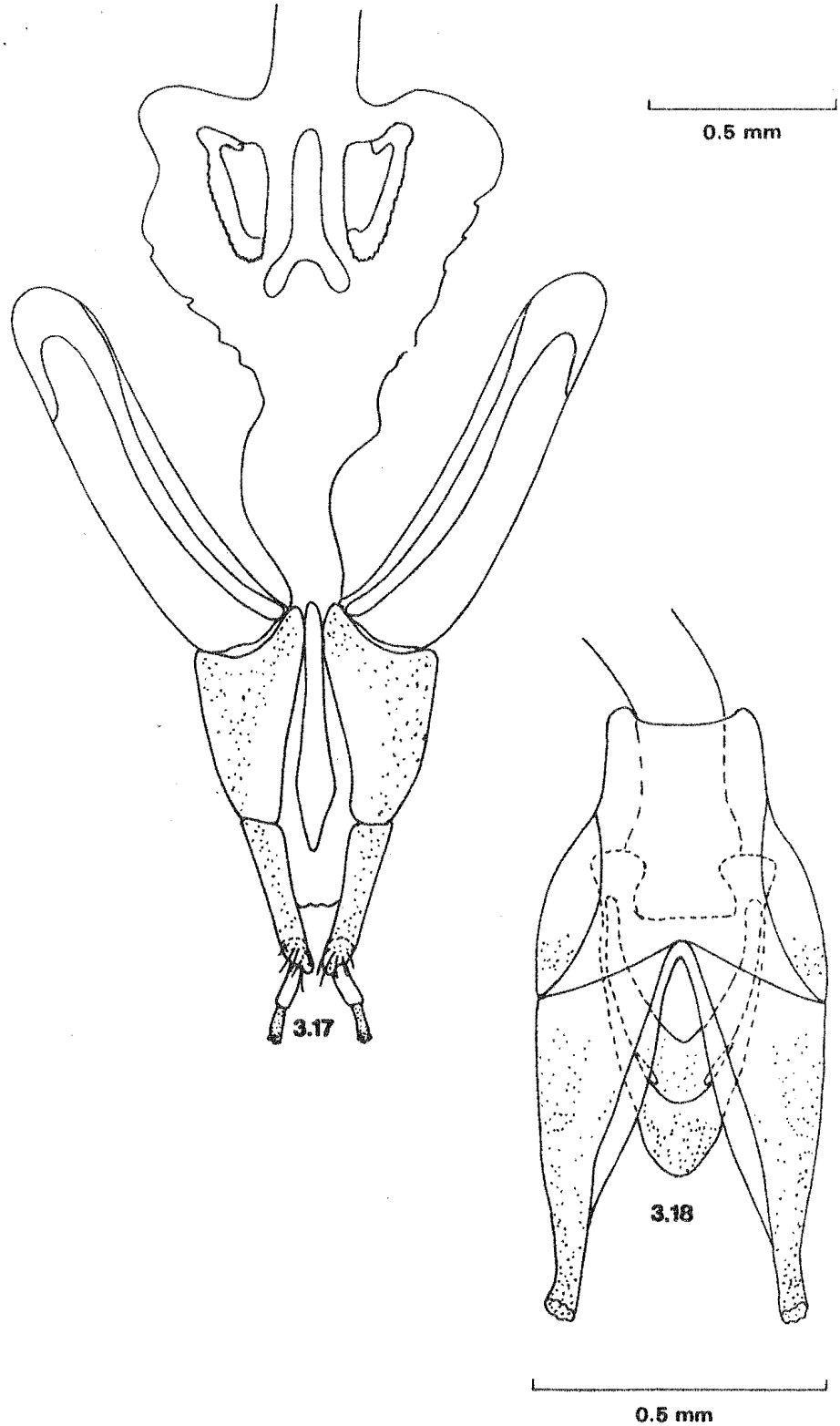


FIGURE 3.16 *Sclerocyphon striatus*, ♀ voucher specimen, ventral view. Scale line = 1 mm.



FIGURES 3.17-3.18 *Sclerocyphon striatus:* (3.17) ♀, external genitalia, ventral view; (3.18) ♂, external genitalia, ventral view. Scale lines = 0.5 mm.

punctate, setose distally, bearing 2-segmented styli. Sclerotised rod, embedded in vaginal wall between hemisternites, expanded distally. Pair of elongate sclerotised plates embedded in anterior dorso-lateral vaginal walls.

Male (Figure 3.18)

Total length 3.9 mm, head width 0.8 mm, pronotal length 0.8 mm, pronotal width 2.05 mm, width between apical angles of pronotum 0.9 mm, scutellar length 0.3 mm, scutellar width 0.35 mm, elytral length 3.0 mm, elytral width 2.45 mm. Similar to female but smaller.

Elytra - relatively shorter than ♀, striations barely visible.

Abdomen - Dense pubescence on segments 2 and 3 parted at midline.

External genitalia (Figure 3.18) - Aedeagus symmetrical, trilobate. Parameres sclerotised, punctate with membranous tips. Penis complex, consisting of 2 sclerites, dorsal sclerite with wide, rounded apex, ventral sclerite smaller, lateral margins with feeble barb near tip.

Last instar larva (Figure 3.19, Pls 3.5-3.9)

Total length 8.0 mm, total width 4.1 mm, length of ninth tergite 1.2 mm, width of ninth tergite 1.6 mm.

General shape - Narrow, elongate thoraco-abdominal shield, widest at metanotum, tapering to tergite 9.

Dorsal surface - Medial region dark brown with some yellow, one large yellow patch on pronotum over each eye, lateral laminae light brown with yellow patches, tergite 9 entirely dark.

Entire marginal fringe of setae with 2 bands visible; narrow, yellow inner band made up of stiff inner section of each seta, wider transparent outer band where setae soft, flexible, tapering to minute point. Trailing edge of all laminae with fringe of fine transparent setae.

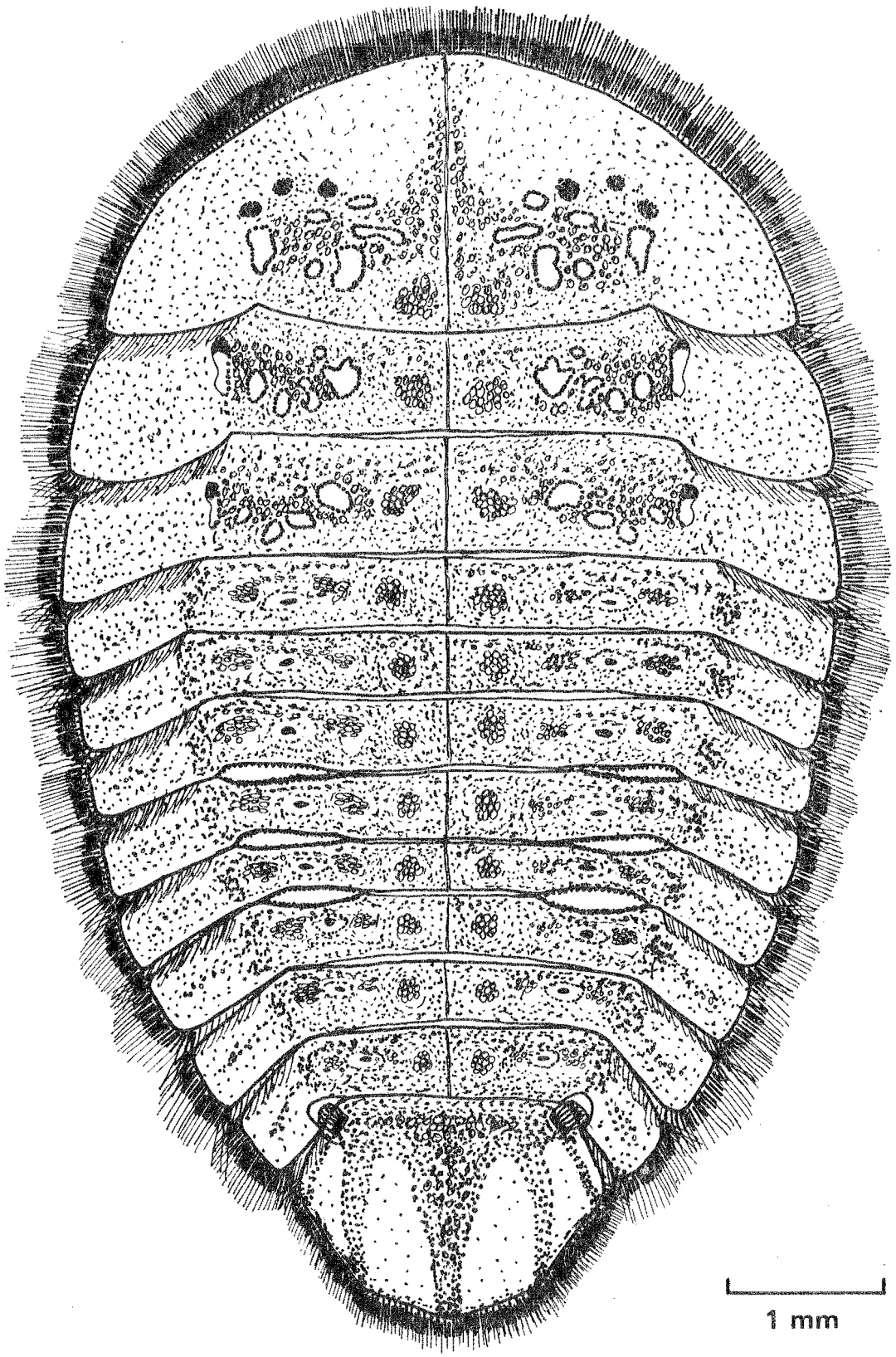
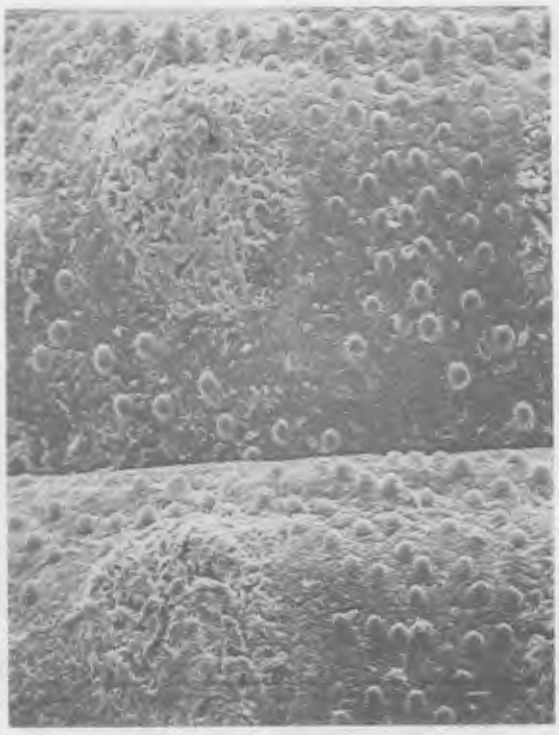
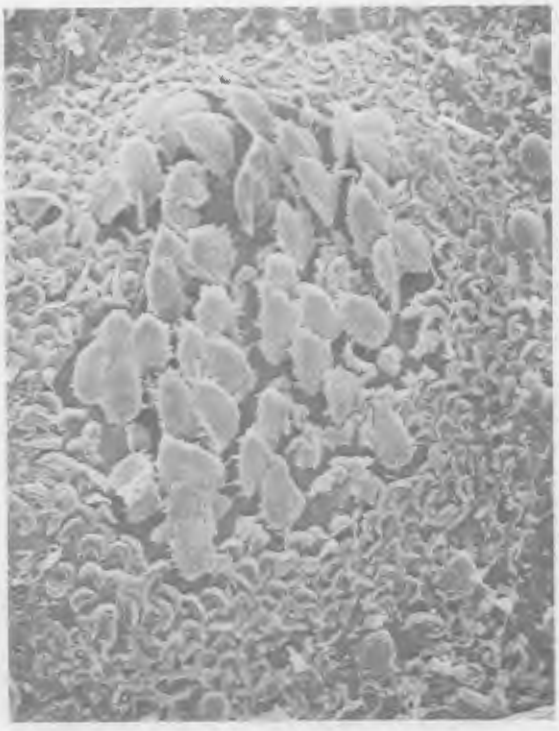


FIGURE 3.19 *Sclerocyphon striatus*, last instar larva, voucher specimen dorsal view. Scale line = 1 mm.



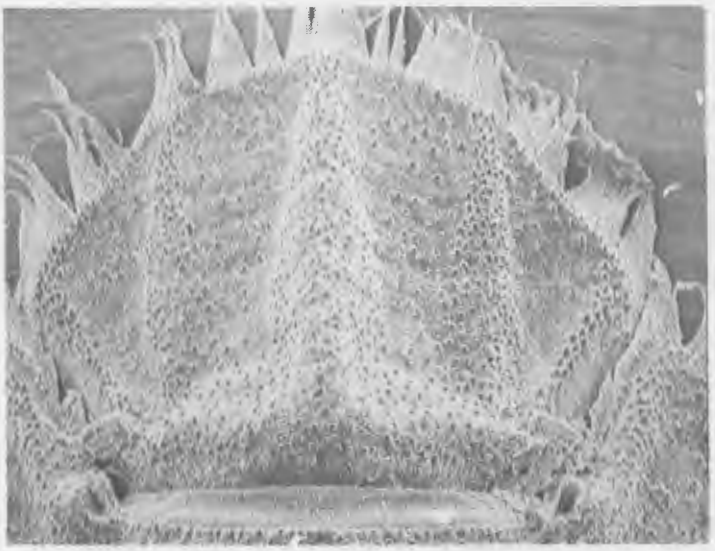
3.5



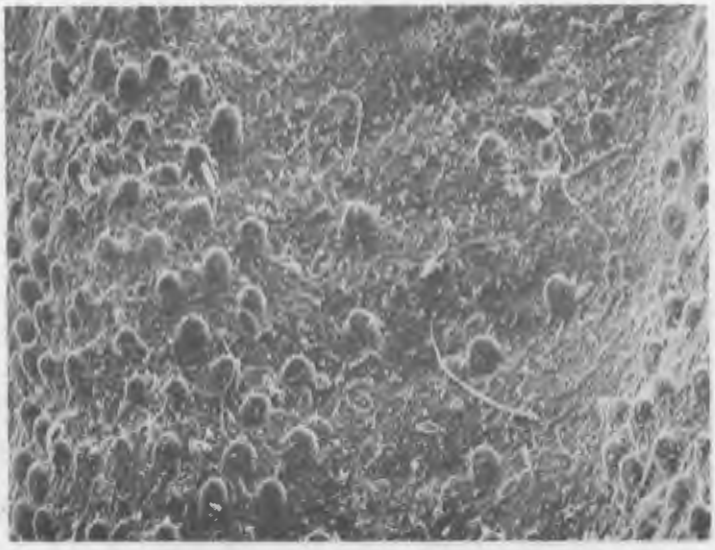
3.6

PLATES 3.5-3.6 *Sclerocyphon striatus*, last instar larva from Swamp Ck: (3.5) clumps of mucous-coated trichoid sensilla in mid-dorsal region of abdominal tergites 4 and 5, x 120; (3.6) clump of mucous-coated trichoid sensilla , x 250.

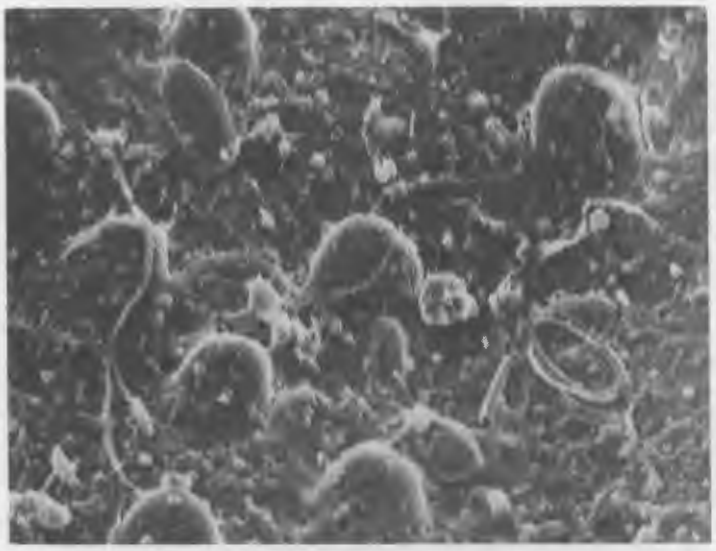
3.7



3.8



3.9



PLATES 3.7-3.9 *Sclerocyphon striatus*, last instar larva from Swamp Ck, tergite 9: (3.7) x 40; (3.8) x 200; (3.9) x 650.

Cuticular beads dense in medial region, sparser on lateral laminae, dense, dark clump of beads at junction of each lamina and body on tergites 1-8. Beads rounded apically.

Pores scattered over entire dorsal surface, densest regions, coated with shining grey mucus, between pits on pro-, meso- and metanotum and on two slightly upraised, oval regions either side of ecdysial scar on each side of sagittal line on tergites 1-8.

Twelve paired groups of trichoid sensilla in medial region, one group to each side of sagittal line on each thoracic and abdominal segment. Discrete sensilla visible only with scanning electron microscopy (Pls 3.5, 3.6). Beneath the light microscope each group visible as circular shining region, outlined by a ring of pores, the two groups of each pair widely separate with derm beneath light coloured.

Pronotum with 5 pairs of irregular pits and 4 pairs of circular pits (lateral 3 dark) in a semi-circle, anteriorly. Meso- and metanotum with 6 pairs of irregular pits. Most pits yellow, outlined by beads.

Three pairs of gin traps present on adjoining margins of tergites 3-4, 4-5 and 5-6. Posterior pair narrower than anterior pairs.

Tergite 9 (Pls 3.7-3.9) with 3 upraised ridges, central ridge pronounced, all ridges densely covered with cuticular beads. Posterior margin with 4 sinuosities, one each side of central ridge and between lateral ridges and lateral margins. Margin at apex of central ridge pointed or rounded. Lateral margins gently curving.

Diagnosis

Adults can be distinguished by the following combination of characters; elongate, subconvex body, "velvet" appearance of dorsal surface created by a dense covering of pubescence over a moderately shining derm, and two feeble lateral barbs on the ventral penile sclerite or small elongate vaginal plates. Males can also be distinguished

by the midline parting in pubescence on sternites 2 and 3.

Larvae can be distinguished on the following combination of characters; 3 gin traps, tergite 9 with 3 ridges, central ridge pronounced, posterior margin with 4 sinuosities, circular clumps of trichoid sensilla medially and uniform covering of cuticular beads.

Comments

The specific epithet is not diagnostic as several other species (described below) exhibit more pronounced elytral striations. Lea (1895) in his description of the holotype male noted

> "...second and third abdominal segments feebly carinate in middle...",

this has not been observed here; however, the parting in pubescence at the midline of sternites 2 and 3 may have been misinterpreted as carina.

The larva, described here for the first time, was linked to the adult by laboratory rearing. The common narrow elongate form is described but a wider form also exists, usually possessing a distinctive colour pattern, of 3 dark brown bands separated by three yellow bands, on the dorsal surface. This form has been included within *S. striatus* on the basis of tergite 9 morphology; however, laboratory rearing of adults from this larval form is needed to verify this inclusion.

S. striatus is widely distributed in Victoria and eastern New South Wales. Larval densities can be extremely high and larvae have been found in both lowland and alpine streams.

Sclerocyphon serratus Lea

Sclerocyphon serratus Lea, 1895, p.598

Material Examined

Types - NEW SOUTH WALES: holotype ♀ (?), Tamworth, SAM.

Comments

Most of the abdomen and elytra of this specimen was missing and positive identification of other material from this type was not easily carried out. No specimens in the collections studied matched the description given by Lea sufficiently well enough to be identified as *S. serratus*. Several specimens identified by previous workers as *S. serratus* were not considered to be valid as a number of misidentifications by earlier workers had been revealed in the course of this study. These were probably due to both the general nature of the early descriptions and the morphological similarity of many of the species of *Sclerocyphon*.

Extensive collecting of adults and larvae of *Sclerocyphon* in the Tamworth region, plus rearing of adults in the laboratory, is the first step required to elucidate the exact form of this species. Possibly larval types described later in this work, in particular *S.* type B from southern Queensland and *S.* type E from a creek east of Nundle, near Tamworth, may be the larval form of *S. serratus* but until laboratory rearing of adults from these larvae is achieved no positive conclusions can be made.

Sclerocyphon basicollis Lea

(Figures 3.20-3.24, Pls 3.10-3.12)

Sclerocyphon basicollis Lea, 1895, p.599

Material Examined

Types - NEW SOUTH WALES: holotype ♂, Tamworth, SAM; paratype ♂, Tamworth, SAM.

Voucher specimens - NEW SOUTH WALES: 1 ♀ (with pupal and larval exuviae), Rocky R. E of Tenterfield, 28.*i*.1980, J.A. Smith, emerged in lab. 8.*iii*.1980, NMV; 1 ♂, Williams R., 1926, H.J. Carter, SAM; 7 L, Port Hacking R., Royal National Park, 19.*i*.1980, J.A. Smith, NMV.

Other material examined - NEW SOUTH WALES: 2 ♂♂, Williams R., Oct. 1926, H.J. Carter, ANIC; 1 ♀, Pe, Le, 35 L, Rocky R. E of Tenterfield, 28.*i*.1980, J.A. Smith, emerged in lab. 27.*iii*.1980; 1 ♂, Pe, Le, Rocky R. E of Tenterfield, 28.*i*.1980, J.A. Smith, emerged in lab. 8.*iii*.1980, 1 ♀, Pe, Le, Tunks Ck, 29.*xii*.1978, G. Edgar, emerged in lab. 28.*iii*.1979; 21 L, Trib. of Rocky R.,E of Tenterfield, 28.*i*.1980, J.A. Smith; 61 L, Peel R., Nundle, E of Tamworth, 26.*i*.1980, J.A. Smith; 1 L, Pages R., Murrunrundi, New England Hwy, 26.*i*.1980, J.A., J.N. Smith; 1 L, Quirindi Ck on Wallabadah Ck Rd, 1 km upstream of Wallabadah, 29.*iv*.1981, P.S. Lake, D. Coleman; 4 L, Trib. of Port Hacking R. above waterfall in McKell Ave, 19.*i*.1980, J.A. and J.N. Smith; 10 L, Trib. of Lane Cove R., Lady Game Drive, Killara, Sydney, 23.*i*.1980, J.A., J.N. Smith; 6 L, Colongolook R., at Princes Hwy, 120 km N of Newcastle, 5.*ii*.1980, J.A., J.N. Smith; 6 L, Yellow Pinch Ck, at Princes Hwy, between Merimbula and Bega, 15.*i*.1980, J.A., J.N. Smith; 9 L, Ck in Moreton National Park, W of Nowra, 18.*i*.1980, J.A., J.N. Smith; 6 L, Armidale, 22.*iii*.1963, CW; 2 L, Berowra Ck, Galston Gorge, 27.*xii*.1978, G. Edgar; 2 L, Kara Ck, 5 mi. W Berridale, nr Cooma,

11.*x*.1978, A. Glaister; 2 L, Rushs Ck, nr Cooma, 12.*x*.1978, A. Glaister; 1 L, Umarallar Ck, nr Cooma, 10.*x*.1978, A. Glaister; VICTORIA: 27 ♀♀, 14 ♂♂, South Morang, 24.*xi*.1928, J.E. Dixon, NMV; 1 ♂, Goulburn R., Alexandra, 7.*xi*.1927, J. Clark, NMV; 1 ♀, Goulburn R., Alexandra, date?, coll.?, NMV; 1 ♂, Aberfeldy R., 10 km NNW of Walhalla, 27.*xi*.1977, A.A. Calder, NMV-SD; 2 ♀♀, 1 ♂, Macalister R., 9 km NNE of Heyfield, 4.*xii*.1976, A.A. Calder, NMV-SD; 1♂, Macalister-Caledonia R. Jn, 6.*xii*.1977, NMV-SD; 1 L, Macalister-Wellington R. Jn, 6.*v*.1977, NMV-SD; 3 L, Wellington R. 23.5 km NNE of Licola on Tamboritha Rd, 25.*ii*.1978, NMV-SD; 1 L, Shaws Ck, Bennison Plains, 15.*xi*.1977, NMV-SD; 11 L, Aberfeldy R., Donellys Ck track, 29.*xi*.1976-13.*ii*.1977, NMV-SD; 4 L, Thomson R., Bells Clearing, 13.*viii*.1977-28.*ii*.1978, NMV-SD; 2 L, Thomson-Jordan R. Jn, Swingler Portal, 1.*v*.1977, NMV-SD; 1 L, Thomson R - Blackberry Ck Jn., Jericho, 28.*xi*.1976, NMV-SD; Thomson R, Thomson-Jordan R., Divide Rd, 1.*ii*.1976, NMV-SD; 51 L, Mitta Mitta R. sites (Appendix A) 1976-1978, NMV-SD; 5 L, Plenty R, Mernda, 16.*xi*.1979, J. Smith, CIT; 2 L, Plenty R., Mernda, 16.*xi*.1979, J. Smith, CIT; 2 L, Maribyrnong R., Sydenham Park, 1980, V. Brown, MMBW. AUSTRALIAN CAPITAL TERRITORY: 1 ♂, Cotter R., 14.*xii*.1929, A. Tonnoir, ANIC. QUEENSLAND: 2 ♂♂, Upper Brookfield, nr Brisbane, 3.*vi*.1967, G. Monteith, QU; 1♀ (?) Highvale, 8.*vii*.19?, A. Diatloff, QU; 2 ♀♀, 3 ♂♂, Kuranda, 10.*viii*.1904, Koebele Collection, BPBM; 3 ♂♂, Hambledon, Nov. 1921, Pemberton Collection, BPBM; 1 L, Yandina, 23.*viii*.1958, D. Ogg, QU; 1 L, Obi Obi Ck, 12 km SE Kenilworth, 10.*iv*.1979, H.B.N. Hynes; 2 L, stream 2 km NE Cooran, 14.*iv*.1979, H.B.N. Hynes; 1 L (21.*viii*.1979), 1 L (22.*viii*.1979), 1 L (18.*ix*.1979), Miles Platting Rd riffle, Bulimba Ck, Brisbane, Griffith University; 1 L (21.*iii*.1979), 1 L (20.*iii*.1979), 1 L (20.*xi*.1979), 1 L (10.*i*.1980), 1 L (3.*iii*.1980), Kimmax St riffle, Bulimba Ck, Griffith University.

Description

As given by Lea (1895) but with the following additions based on an examination of voucher specimens, and larvae.

Female (Figures 3.20-3.22)

Total length 4.4 mm, head width 0.9 mm, pronotal length 1.0 mm, pronotal width 2.5 mm, width between apical angles of pronotum 2.5 mm, scutellar length 0.3 mm, scutellar width 0.5 mm, elytral length 3.3 mm, elytral width 3.05 mm.

General shape - Nearly circular, broad, convex.

Head - Black with red ring around eye.

Pronotum - Black anteriorly, lighter red-brown at base, irregularly clothed with dense ashen pubescence, where pubescence sparse, shiny punctate derm visible. Lateral margins narrow, flat, yellow, pronotum deflected forwards.

Scutellum - Red-brown, sloping forwards.

Elytra - Uniformly black, small clumps of coarse white pubescence on lateral and apical regions, medial region relatively glabrous, exposed derm very shiny with minute punctures and fine transverse wrinkles. Overall elytra broad, nearly as wide as long, widest at middle, gently convex. Wide shallow impression at lateral margin, in basal third, on each side. Margins yellow, wider at base than apex.

Thorax - Pro-, meso- and metasternum and antecoxal piece brown.

Abdomen (Figure 3.21) - All segments yellow.

External genitalia (Figure 3.22) - Pair of sclerotised hemisternites, punctate, setose distally, bearing 2-segmented styli. Sclerotised rod embedded in vaginal wall between hemisternites fairly broad, expanded distally. Pair of sclerotised plates embedded in anterior dorso-lateral vaginal walls relatively small, narrow.

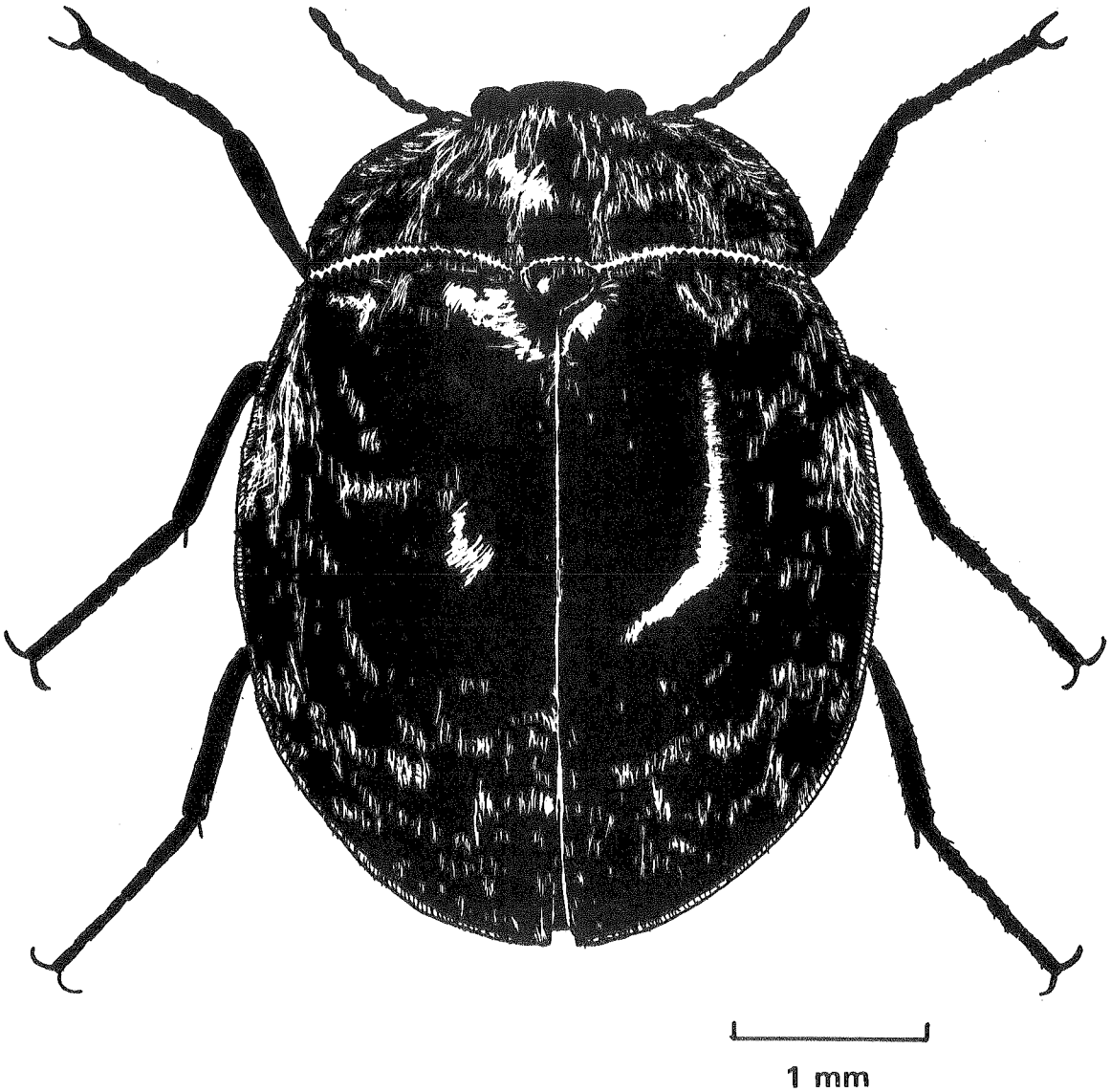


FIGURE 3.20 *Sclerocyphon basicollis*, ♀ voucher specimen, dorsal view. Scale line = 1 mm.

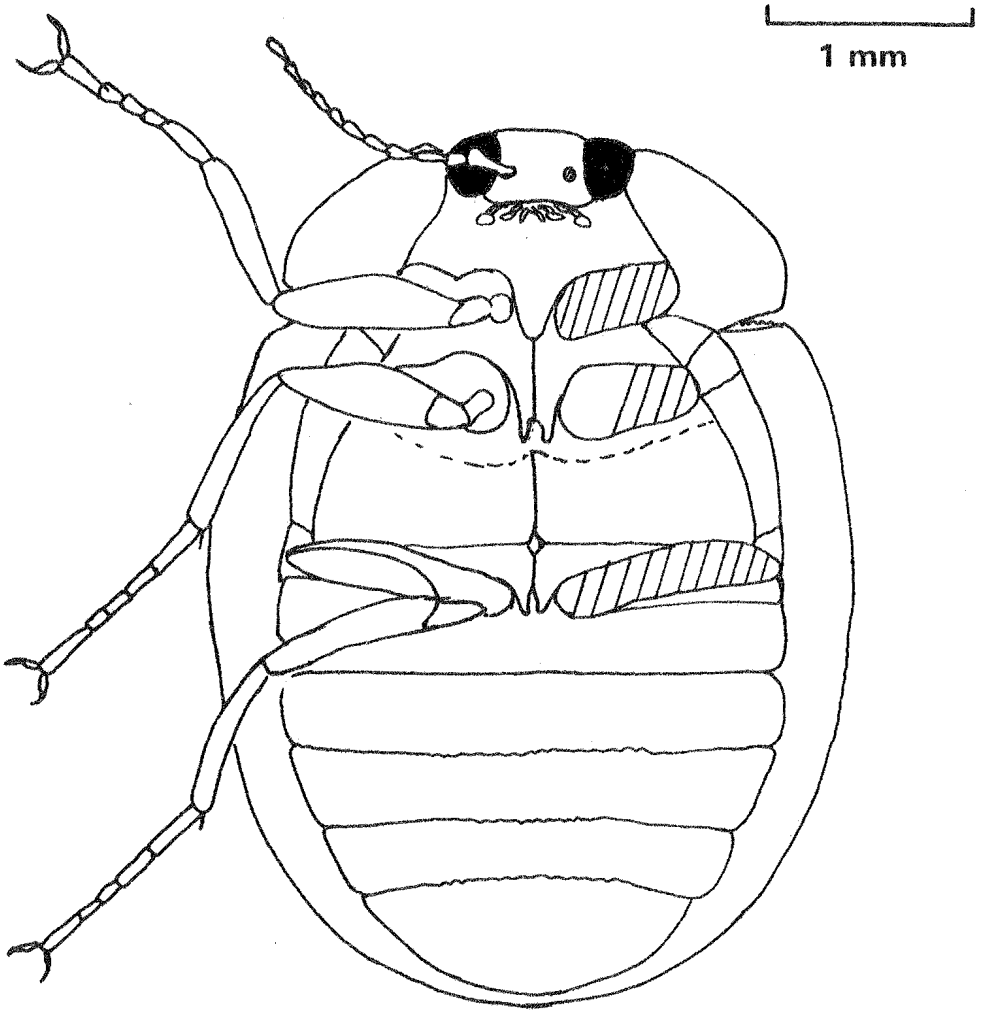


FIGURE 3.21 *Sclerocyphon basicollis*, ♀ voucher specimen, ventral view. Scale line = 1 mm.

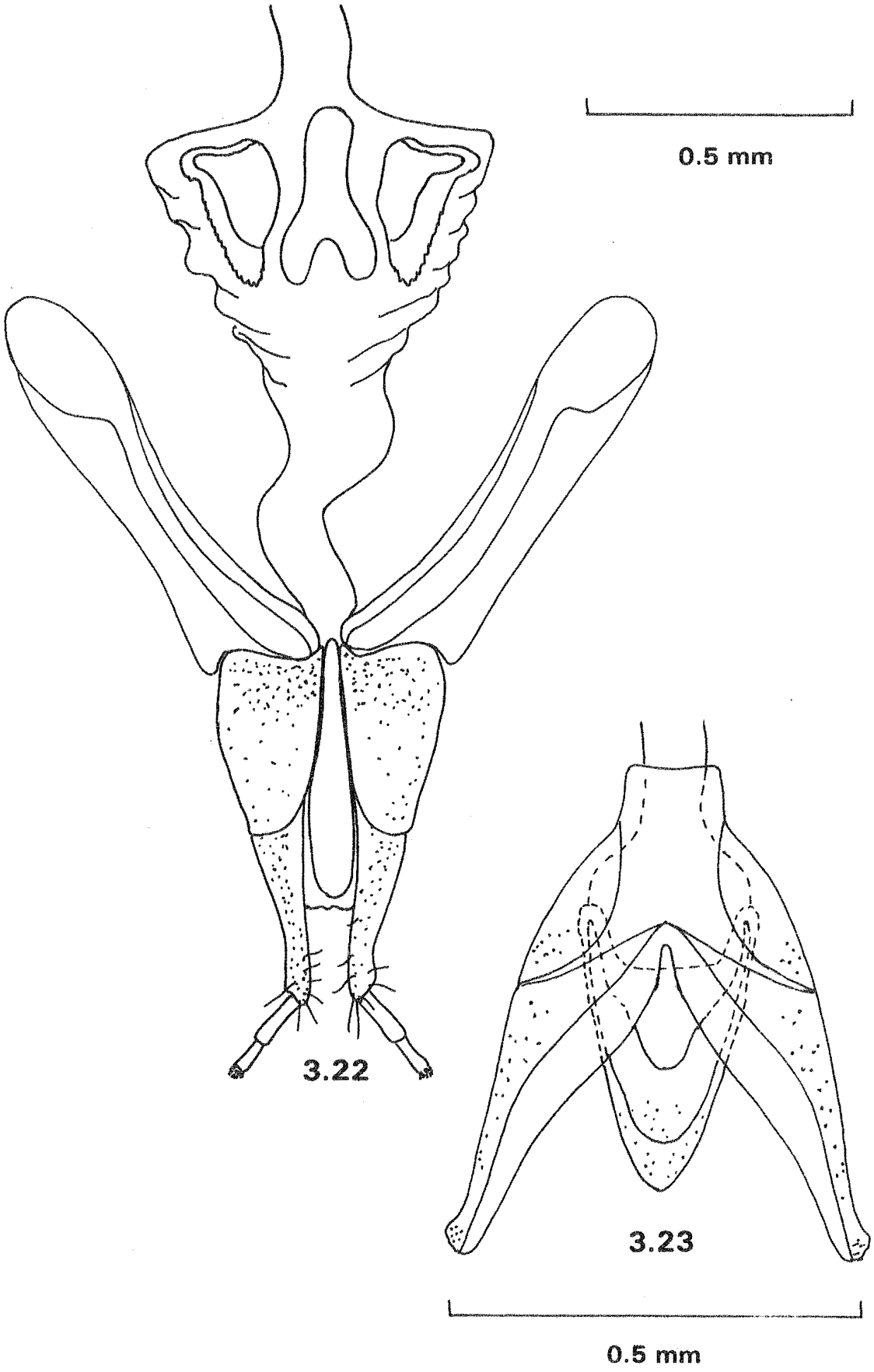


FIGURE 3.22-3.23 *Sclerocyphon basicollis:* (3.22) ♀ external genitalia, ventral view; (3.23) ♂ external genitalia, ventral view. Scale lines = 0.5 mm.

Male (Figure 3.23)

Total length 3.35 mm, head width 0.8 mm, pronotal length 0.7 mm, pronotal width 1.95 mm, width between apical angles of pronotum 0.9 mm, scutellar length 0.15 mm, scutellar width 0.3 mm, elytral length 2.55 mm, elytral width 2.4 mm.

Similar to female but smaller and with nearly entire covering of dense fine white pubescence.

External genitalia (Figure 3.23) - Aedeagus symmetrical, trilobate, parameres sclerotised, punctate with rounded membranous tips. Penis complex, consisting of 2 sclerites, dorsal sclerite with lateral margins tapering to fairly narrow apex, ventral sclerite smaller with widely rounded apex.

Last instar larva (Figure 3.24, Pls 3.10-3.12)

Total length 7.0 mm, total width 3.9 mm, length of ninth tergite 1.1 mm, width of ninth tergite 1.5 mm.

General shape - Elongate-ovate thoraco-abdominal shield, widest at tergite 1, tapering to tergite 9.

Dorsal surface - Medial region dark brown with narrow yellow patches on tergites 2, 3 and 5, 6, 7.

Lateral laminae with alternating strips of colour: brown-yellow-brown-yellow-brown. Tergite 9 dark brown overall.

Entire marginal fringe of setae with 2 bands visible; narrow, brown, inner band made up of stiff inner section of each seta, wide transparent outer band where each seta soft, flexible, tapering to minute point. Trailing edges of all laminae with fringe of fine transparent setae.

Dense uniform covering of dark, sclerotised cuticular beads over entire dorsal surface except for bare narrow strip along posterior margin of lateral laminae of tergites 1-8. Beads relatively small.

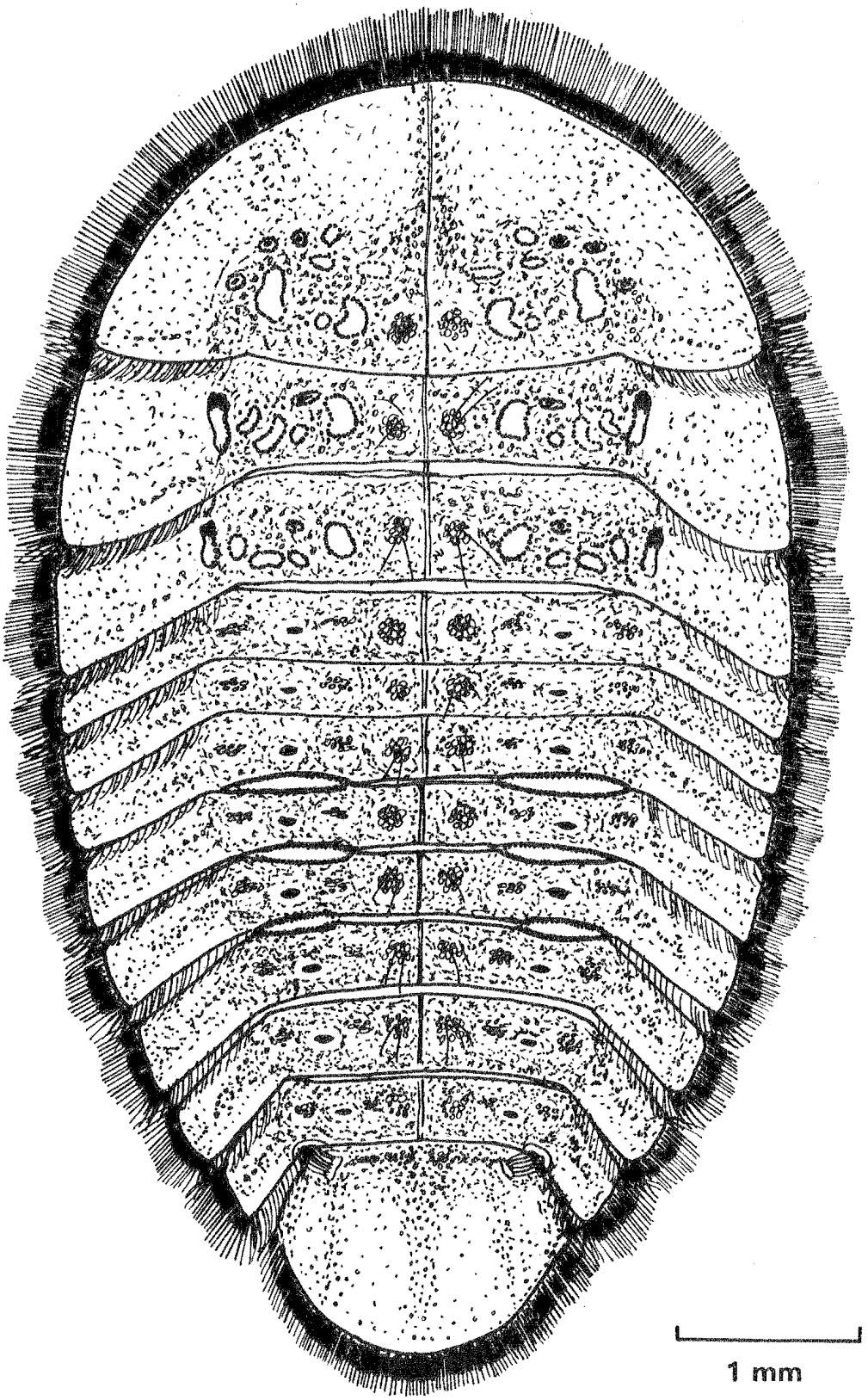
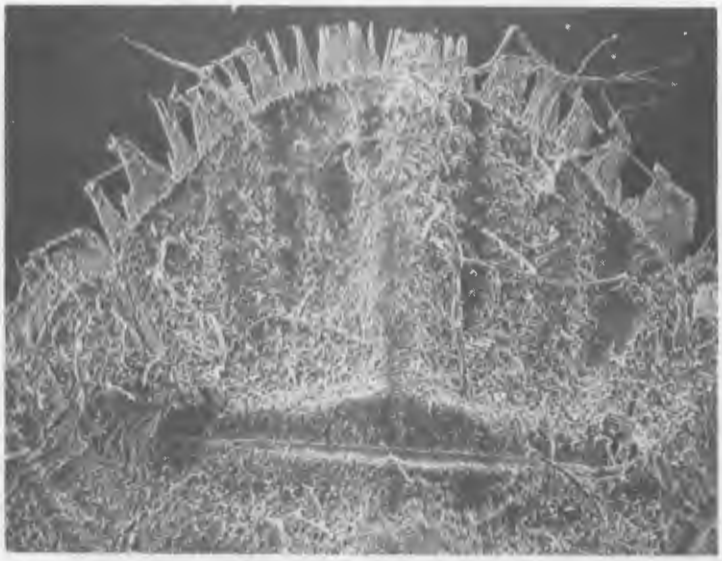
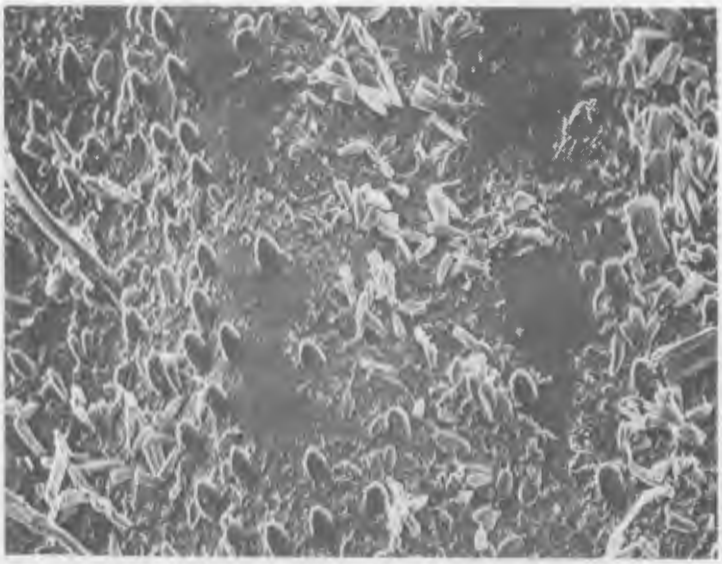


FIGURE 3.24 *Sclerocyphon basicollis*, last instar larva, voucher specimen, dorsal view. Scale line = 1 mm.

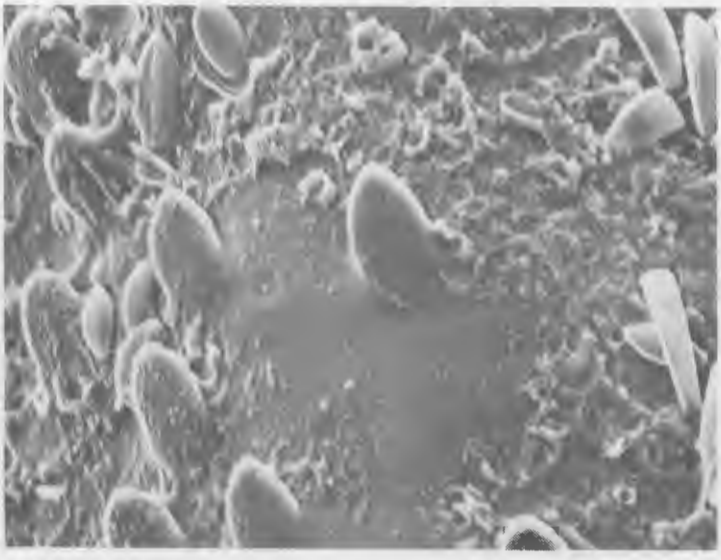
3.10



3.11



3.12



PLATES 3.10-3.12 *Sclerocyphon basicollis*, last instar larva from Port Hacking R, tergite 9: (3.10) x 40; (3.11) x 200; (3.12) x 650.

Pores, visible as shining yellow dots, scattered over entire dorsal surface, densest regions between pits and extending along midline to anterior margin of pronotum, between pits on meso- and metanotum and extending down onto lateral laminae. Two oval clumps of pores on each side of ecdysial scar, each side of midline, and narrow row extending across lateral lamina, on tergites 1-8. Tergite 9 with pores following contours.

Twelve paired groups of trichoid sensilla in medial region, one group to each side of midline on each thoracic and abdominal segment. Discrete sensilla visible only with scanning electron microscopy. Beneath light microscope each group visible as dark, shining, circular, mucous mass, outlined by a ring of shining yellow pores. Some groups with individual hairs projecting from mass, tergites 8 and 9 with smaller clumps.

Pronotum with 5 pairs of irregular pits and 4 pairs of circular pits, lateral 3 dark coloured. Meso- and metanotum with 6 pairs of irregular pits. Most pits yellow, outlined by cuticular beads.

Three pairs of gin traps present on adjoining margins of tergites 3-4, 4-5 and 5-6. Decreasing in width posteriorly.

Tergite 9 with three faintly upraised ridges outlined with cuticular beads, central ridge not reaching posterior margin. Posterior margin produced in a semi-circle with a slight sinuosity each side of medial region. Lateral margins curving to rounded apical angles.

Diagnosis

Adults can be distinguished by the following combination of characters; small size, broad, convex,nearly circular body, dorsal surface with very fine soft white pubescence and shining derm, and very short penile sclerites or short narrow vaginal plates.

Larvae can be distinguished by the following combination of characters; 3 gin traps, tergite 9 with weakly developed central ridge

and regularly curved posterior margin, and the presence of numerous shining yellow pores dorsally.

Comments

The larva, described here for the first time, was linked with the adult by laboratory rearing. While the adult exhibits several very distinctive features (shining derm and convex, nearly circular body) the larva may be easily confused with that of *S. striatus*, being similar in many aspects. The most useful character separating the larvae of the two species is the form of the ninth tergite. The ninth tergite of *S. basicollis* is more feebly ridged and the posterior margin less sinuous than that of *S. striatus*.

Although most adults of *S. basicollis* possess uniformly black pronota some exhibit the two-colour pattern (black medially, yellow laterally) also seen in *S. collaris*.

S. basicollis appears to be predominantly a coastal species, occurring in eastern Victoria and along the entire New South Wales coastline to south-eastern Queensland. It has also been recorded from northern Queensland.

Sclerocyphon collaris (Fabricius)

(Figures 3.25-3.28)

Tritoma collaris, Fabricius, 1775, p.69 n.2.

Sclerocyphon bicolor, Carter, 1919, p.191

Material Examined

Types - QUEENSLAND: holotype ♀, NMV Reg. No. 477, Kuranda, 29.*ix*.1919, NMV. Paratypes: 1 ♂ NMV Reg. No. 478, Kuranda, 29.*ix*.1919, NMV; 1 ♀, Endeavour R., ANIC.

Voucher specimens - QUEENSLAND: 1♀, Kuranda, 22.*i*.1919, F.P. Dodd, SAM; 1♂, Cairns, date?, E. Allen, SAM.

Other material examined - QUEENSLAND: 1♀(?), Kuranda, 29.*ix*.1919, NMV; 1♀, 2 ♂♂, Cairns, date?, E. Allen, SAM; 1♂(?) Kuranda, 22.*i*.1919, F.P. Dodd, SAM; 1 adult (head and pronotum only), N. Queensland, Blackburn's Collection, SAM; 2 ♀♀, Hastings Ck, Biggenden, 6.*xii*.1976, H. Frauca, ANIC.

Description

As given by Carter (1919) but with the following additions based on an examination of voucher specimens: female and male.

Female (Figures 3.25-3.27)

Total length 5.4 mm, head width 1.0 mm, pronotal length 1.1 mm, pronotal width 2.95 mm, width between apical angles of pronotum 1.1 mm, scutellar length 0.45 mm, scutellar width 0.55 mm, elytral length 4.2 mm, elytral width 3.6 mm.

General shape - oval, convex.

Head - Black, yellow ring around eye.

Pronotum - Medial region black, glabrous, very shiny, minutely

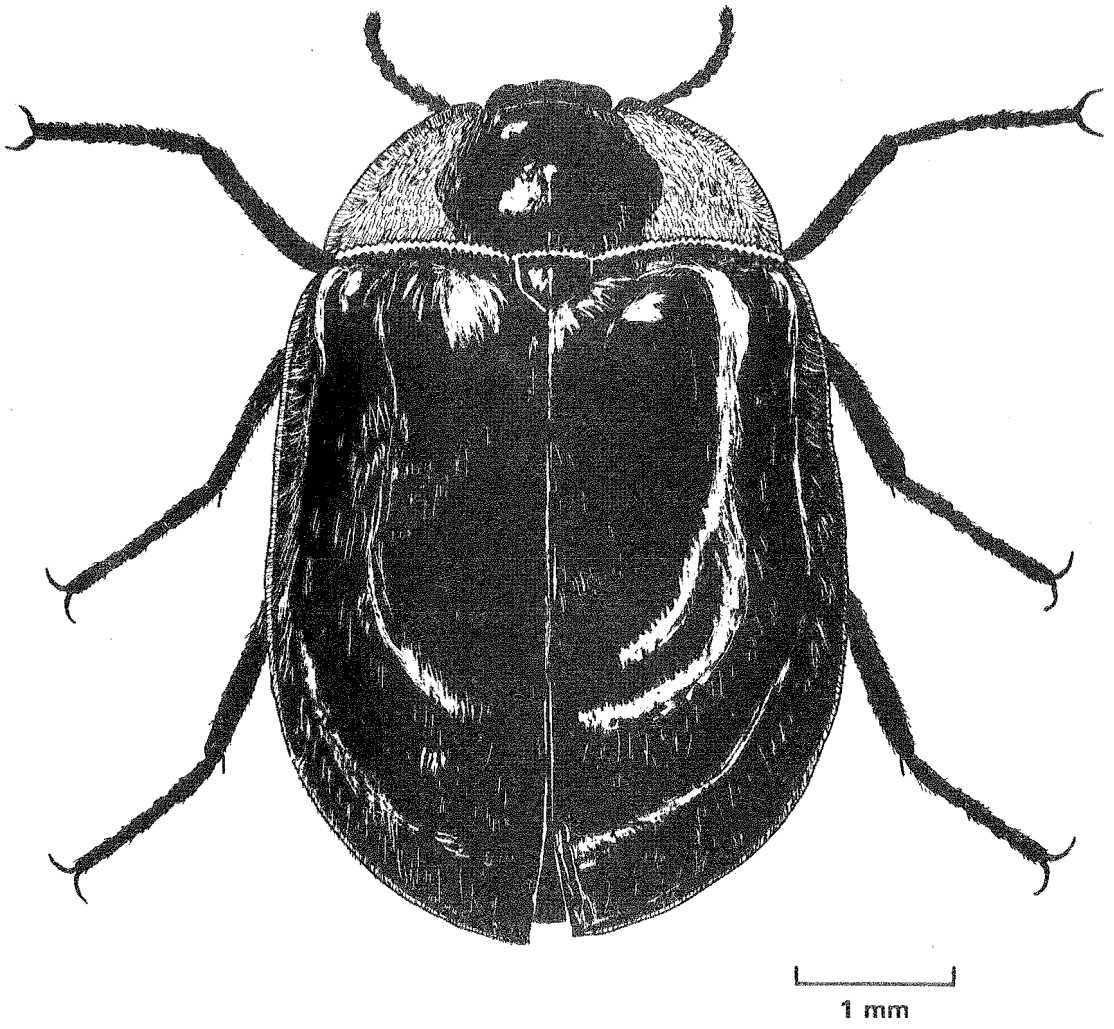


FIGURE 3.25 *Sclerocyphon collaris*, ♀ voucher specimen, dorsal view. Scale line = 1 mm.

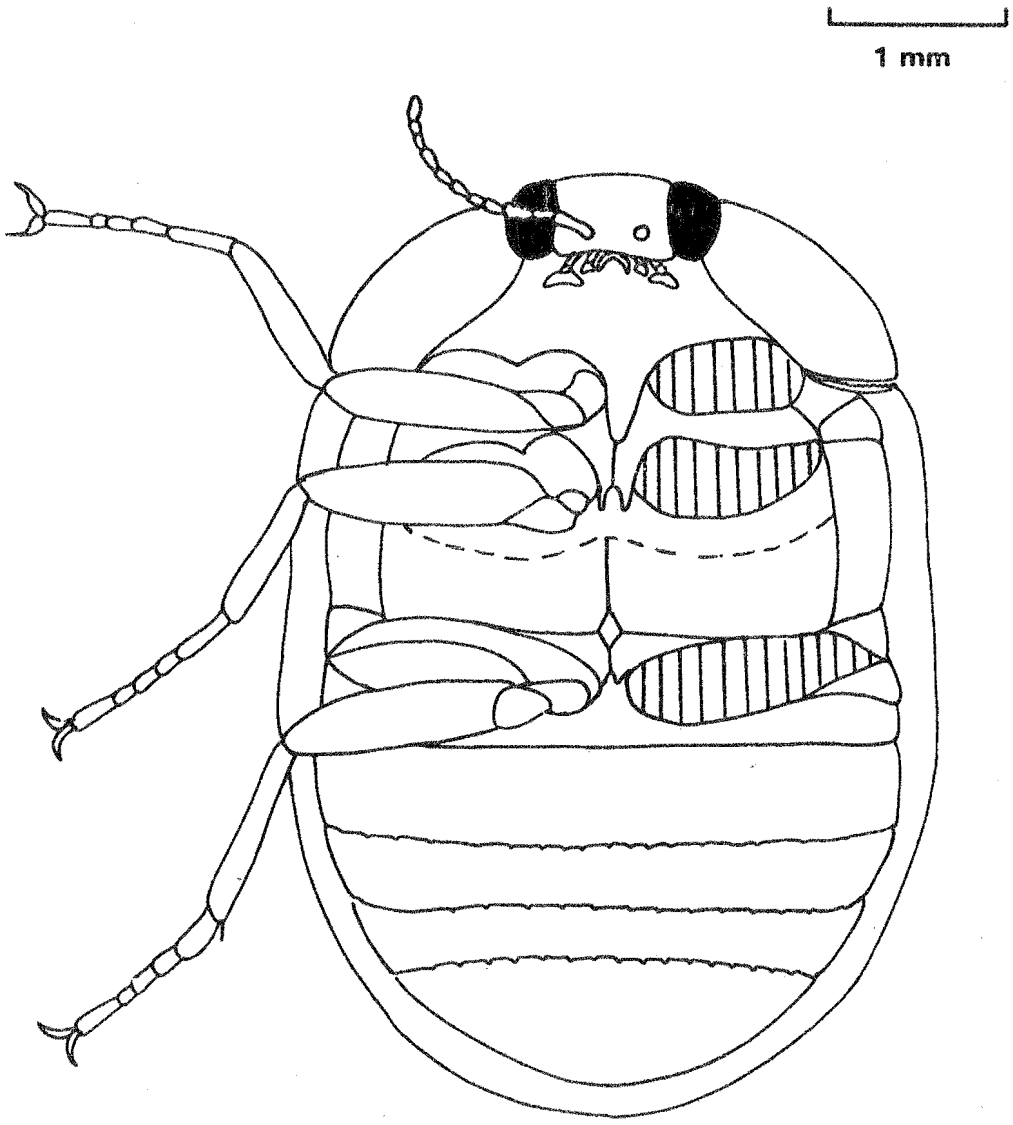
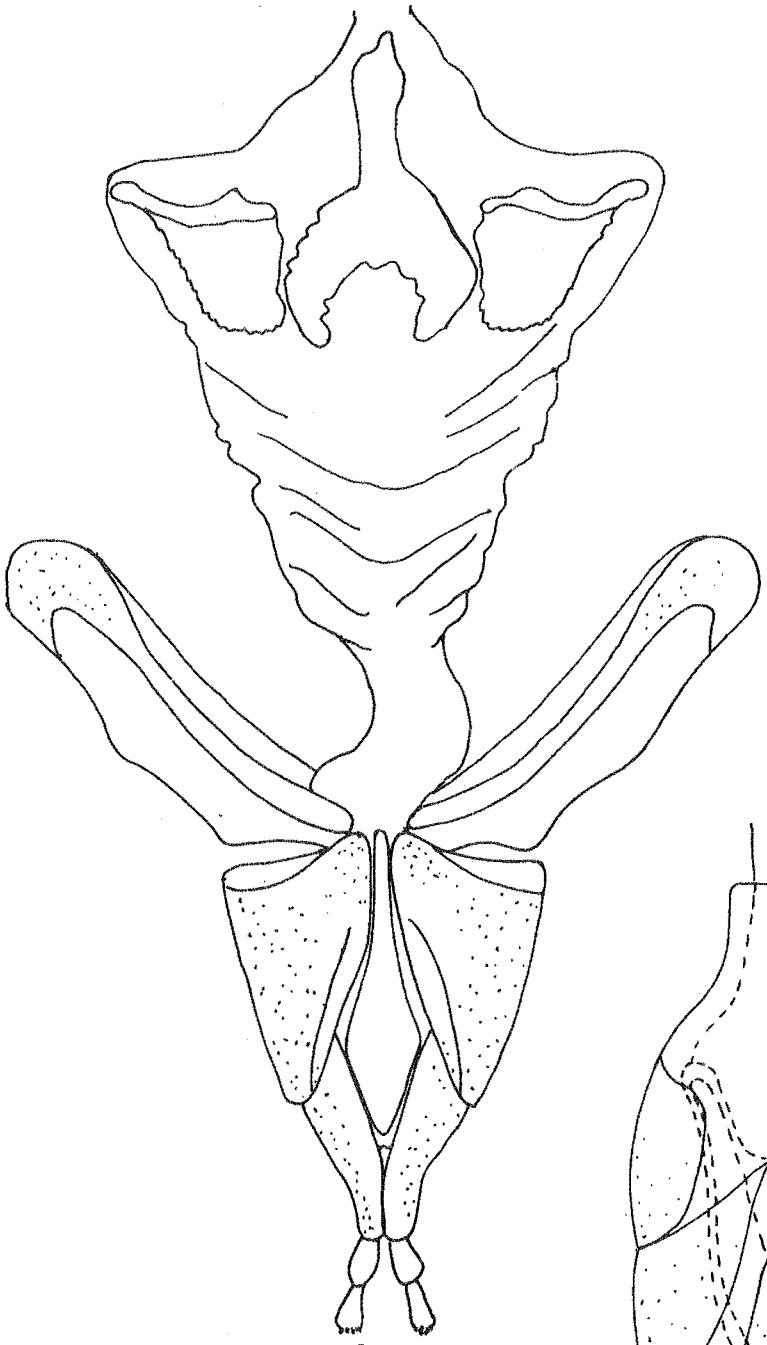


FIGURE 3.26 *Sclerocyphon collaris*, ♀ voucher specimen, ventral view. Scale line = 1 mm.



FIGURES 3.27-3.28 *Sclerocyphon collaris:* (3.27) ♀, external genitalia, ventral view; (3.28) ♂ external genitalia, ventral view. Scale lines = 0.5 mm.

punctate, medial line faintly visible. Lateral third, on each side, yellow, covered with dense fine pubescence. Lateral margins narrow, yellow.

Scutellum - Red-brown, slightly raised, glabrous, shiny.

Elytra - Black overall, but lighter red-black basally and medially. Derm very shiny beneath irregularly scattered, short, fine, ashen pubescence, striations faintly visible laterally, fine transverse wrinkles extending from each side of suture. Deep transverse marginal impression behind high glabrous shoulder, on each side, giving "waisted" effect. Elytra gently dilating to beyond middle, widest at posterior two-thirds.

Legs - Femur black, tibia, tarsi yellow.

Thorax - Pro-, meso- and metasternum black, antecoxal piece yellow.

Abdomen (Figure 3.26) - All segments yellow.

External genitalia (Figure 3.27) - Pair of sclerotised hemisternites punctate, setose distally, bearing 2-segmented styli. Sclerotised rod embedded in ventral vaginal wall between hemisternites narrow proximally, broadly expanded distally. Pair of sclerotised plates embedded in dorso-lateral walls of vagina short and wide, thickly sclerotised anteriorly.

Male (Figure 3.28)

Total length 4.1 mm, head width 0.85 mm, pronotal length 0.9 mm, pronotal width 2.3 mm, width between apical angles of pronotum 1.05 mm, scutellar length 0.3 mm, scutellar width 0.4 mm, elytral length 3.1 mm, elytral width 2.95 mm.

Similar to female but smaller.

Elytra - Derm red-brown, very shiny, pubescence sparse.

External genitalia (Figure 3.28) - Aedeagus symmetrical, trilobate. Parameres sclerotised, punctate with round membranous tips. Penis complex, consisting of 2 sclerites, dorsal sclerite with lateral margins tapering to narrow, rounded apex, ventral sclerite smaller with widely rounded apex.

Diagnosis

Adults can be distinguished by the following combination of characters; pronotum with medial third black, lateral thirds yellow, very shiny, black, strongly convex and "waisted" elytra, and short wide penile sclerites or vaginal plates with narrow anterio-lateral projections and thicker sclerotisation anteriorly.

Comments

One beetle of this species was collected by Sir Joseph Banks during the historic voyage of the "Endeavour" (1768-1771) under the command of Captain James Cook and is now part of the Banks Collection held at the British Museum (Natural History). The "Endeavour", whilst sailing up the east coast of Australia, stopped for brief periods of time at Botany Bay, Bustard Bay and Thirsty Bay and for two months at Endeavour River (Cooktown) while the ship was repaired after running aground on corals. A. Musgrave, quoted by Radford (1980), has suggested that it was probably too late in the season for collecting insects at Botany Bay (New South Wales) and therefore most insects in the Banks Collection were probably taken at Endeavour River (north Queensland), although some may also have been taken at Bustard and Thirsty Bays (Queensland).

The locality of the specimen held in the British Museum (Natural History) is merely given as "*nova Hollandia*"; however, in the light of the above knowledge, the presently known distribution of the species

(Chapter 4) and the fact the specimen was similar to the Carter paratype from Endeavour River in almost all aspects (Dr. R. D. Pope, British Museum (Natural History), pers. comm, 1978) suggests that the Banks' specimen may well have been collected at Endeavour River.

Fabricius named the specimen *Tritoma collaris* in his *Systema Entomologiae* in 1775 but Radford (1980) recognised the synonymy with *Sclerocyphon bicolor*. Although "*collaris*" takes precedence as the specific epithet, "*bicolor*" was very apt as the two colours (black and yellow) on the pronotum are very distinctive.

The distinctive pronotal colour pattern and very shiny "waisted" elytra makes this species the most easily recognisable member of *Sclerocyphon*. No larval form has been linked with the adult and only a small number of beetles have been collected. At present this species appears to be restricted to northern Queensland.

Sclerocyphon aquaticus Lea

(Figures 3.29-3.33, Pls 3.13-3.15)

Sclerocyphon aquaticus Lea, 1919, p.252

additions to description, Smith, 1981, p.277

Material Examined

Types - TASMANIA: ♀ holotype, 1 ♀ paratype, Waratah; 2♀♀ paratypes,* Hobart, In SAM.

Voucher specimens - TASMANIA (all Hellyer R., 8015 837298, 27.*ii*.1979); 1 ♂ (TM Reg. No. F879), 1 ♀ (TM Reg. No. F880), larvae (TM Reg. No. F881), in TM; other ♂♂, ♀♀ and larvae in SAM, NMV and ANIC.

Other material examined - TASMANIA: 4 ♂♂, 25 ♀♀, Gordon R., 1.5 km below Angel Cliffs, 8012973811, 12.*ii*.1977, D. Coleman, G. Edgar; 3 ♂♂, 19 ♀♀, Gordon R., 400 m above Howards Ck junction, 8012991735, 5.*ii*.1977, D. Coleman, G. Edgar, A. Richardson; 1 ♂, 4 ♀♀, Gordon R., 200 m above Denison R., 8012046677, 8.*ii*.1977, D. Coleman, G. Edgar; 4 ♂♂, 6 ♀♀, Hellyer R., 8015837298, reared in lab., Jan. 1978; 8 ♂♂. 9 ♀♀, Sorell Ck, Mt. Wellington, 8312 124609, reared in lab. Jan. 1979; 3 ♂♂, 2 ♀♀, Horseshoe Bend Ck, 8513850261, reared in lab. Nov.1978; 1 ♂, Wandle R., 8015813200, reared in lab. Oct.1978; 2 ♀♀, Tullochgorum Ck, 8414750862, reared in lab. Nov.1978; 2 ♂♂, West Swan R., 8514 847606, Aug.1978. Plus larvae collected from 56 localities (Figure 4.22) (for brevity larval localities are not listed here).

Description

As given by Lea (1919) but with the following additions based on an examination of voucher specimens; ♀, ♂ and larvae.

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* Examination of Lea's 2♀♀ paratypes from Hobart revealed that they are not *S. aquaticus* but *S. secretus*.

Female (Figures 3.29-3.31)

Total length 6.8 mm, pronotal length 1.1 mm, pronotal width 5.7 mm, elytral length 4.1 mm, elytral width 3.3 mm.

General shape - Elliptic, convex beetle.

Pronotum - Black, derm shining beneath sparse, irregularly distributed pubescence, medial region relatively glabrous, gently convex.

Elytra - Black, derm shining beneath irregularly distributed ashen pubescence. Elongate, widest beyond middle. Large, deep marginal impression behind shoulder, on each side, giving elytra "waisted" appearance. Short transverse wrinkles extending laterally from suture in basal two-thirds. Striations obscure.

Thorax (Figure 3.30) - Metasternum with transverse suture produced in curve each side of midline above antecoxal piece.

Abdomen (Figure 3.30) - Segments 1-4 with black patches outlined with yellow. Segment 5 black with yellow medially.

External genitalia (Figure 3.31) - Pair of sclerotised hemisternites punctate, setose distally, bearing 2-segmented styli. Sclerotised rod embedded in vaginal wall between hemisternites, expanded at middle, broader posteriorly than anteriorly. Pair of elongate sclerotised plates embedded in anterior dorso-lateral walls of vagina.

Male (Figure 3.32)

Total length 5.5 mm, pronotal length 0.9 mm, pronotal width 2.4 mm, elytral length 4.4 mm, elytral width 3.2 mm.

Similar to female but smaller, less elongate.

External genitalia (Figure 3.32) - Aedeagus symmetrical, trilobate. Parameres large, sclerotised with rounded membranous tips. Penis complex, consisting of 2 sclerites, dorsal sclerite with lateral

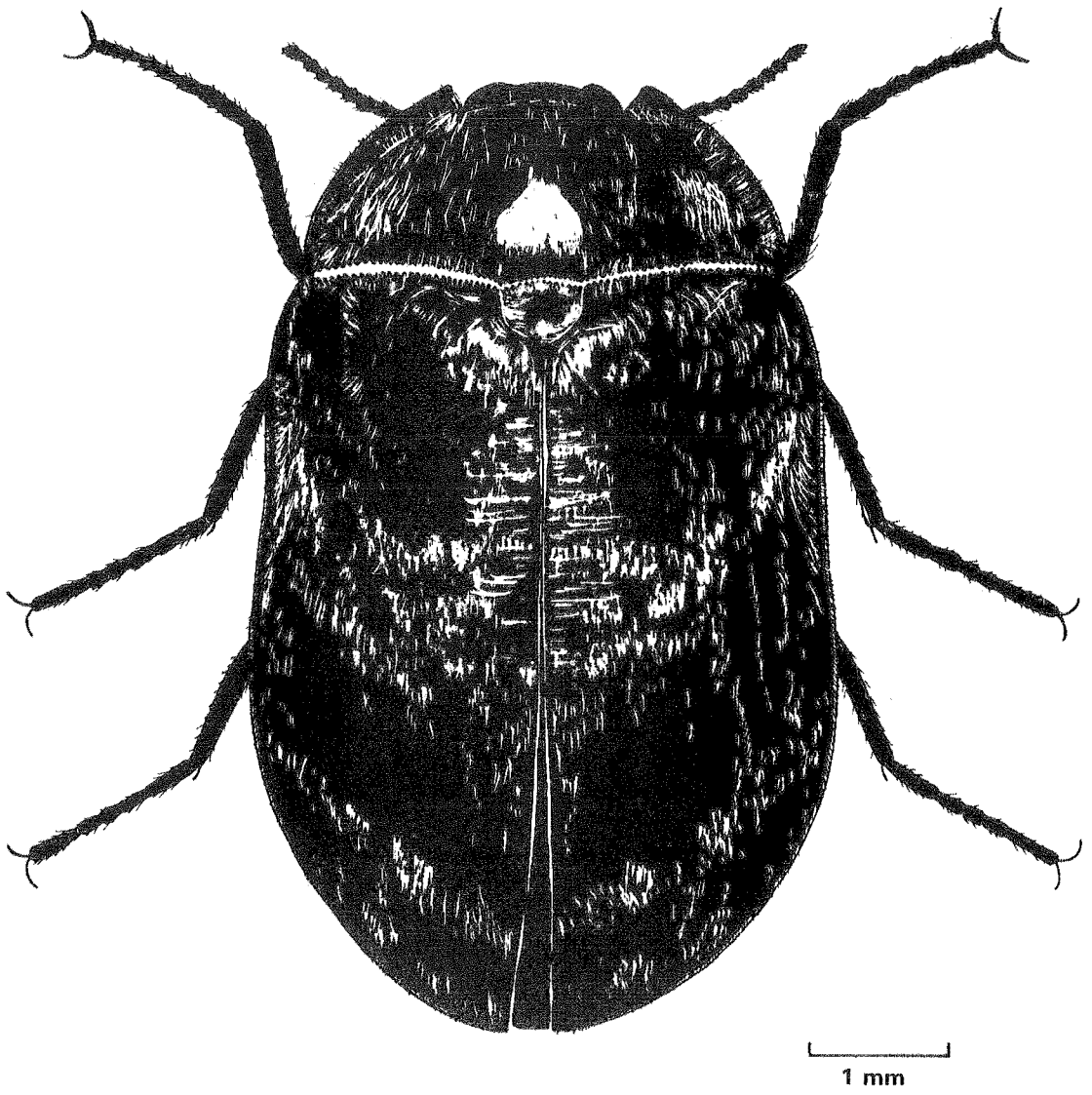


FIGURE 3.29 *Sclerocyphon aquaticus*, ♀ voucher specimen, dorsal view. Scale line = 1 mm.

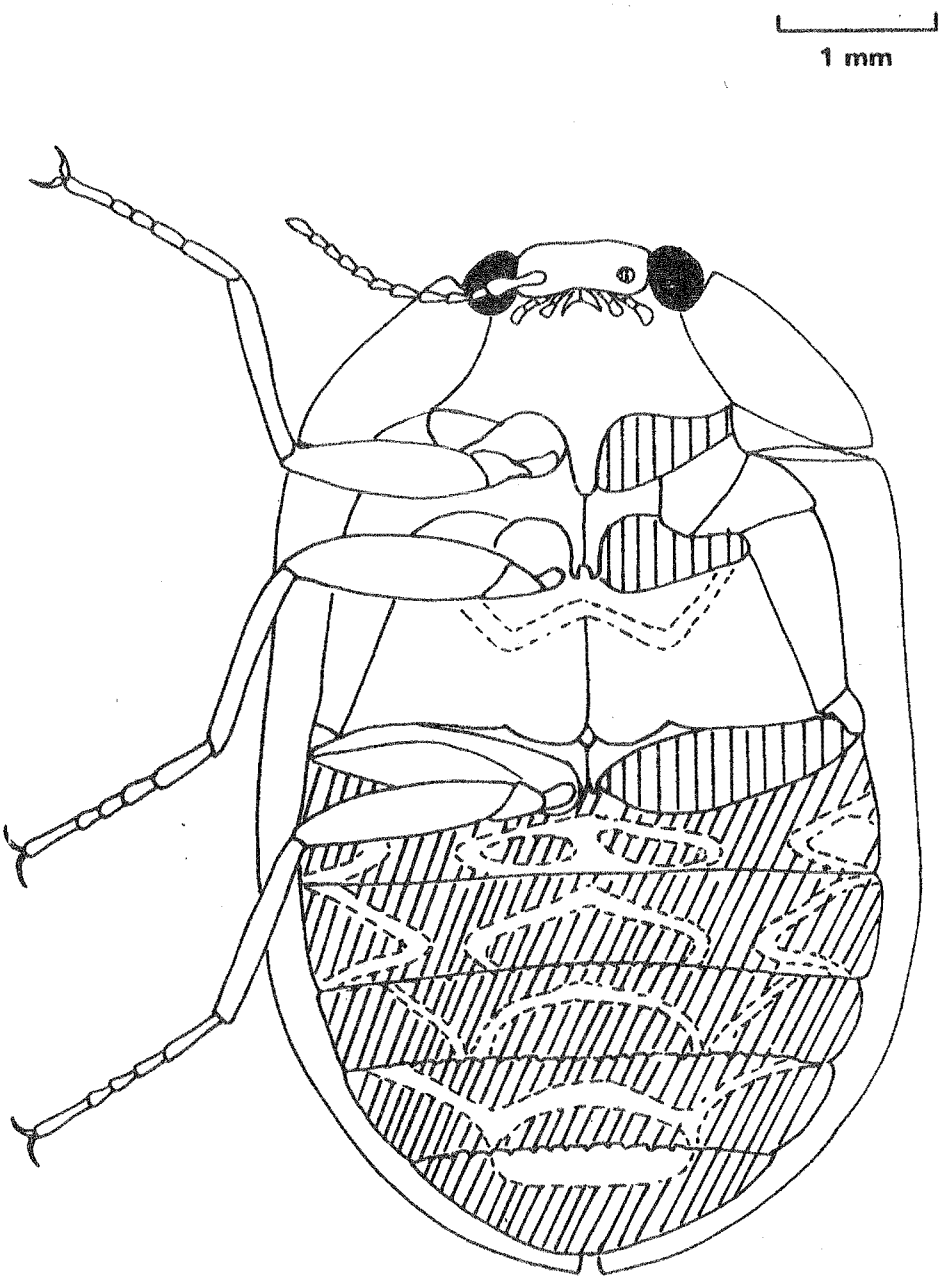
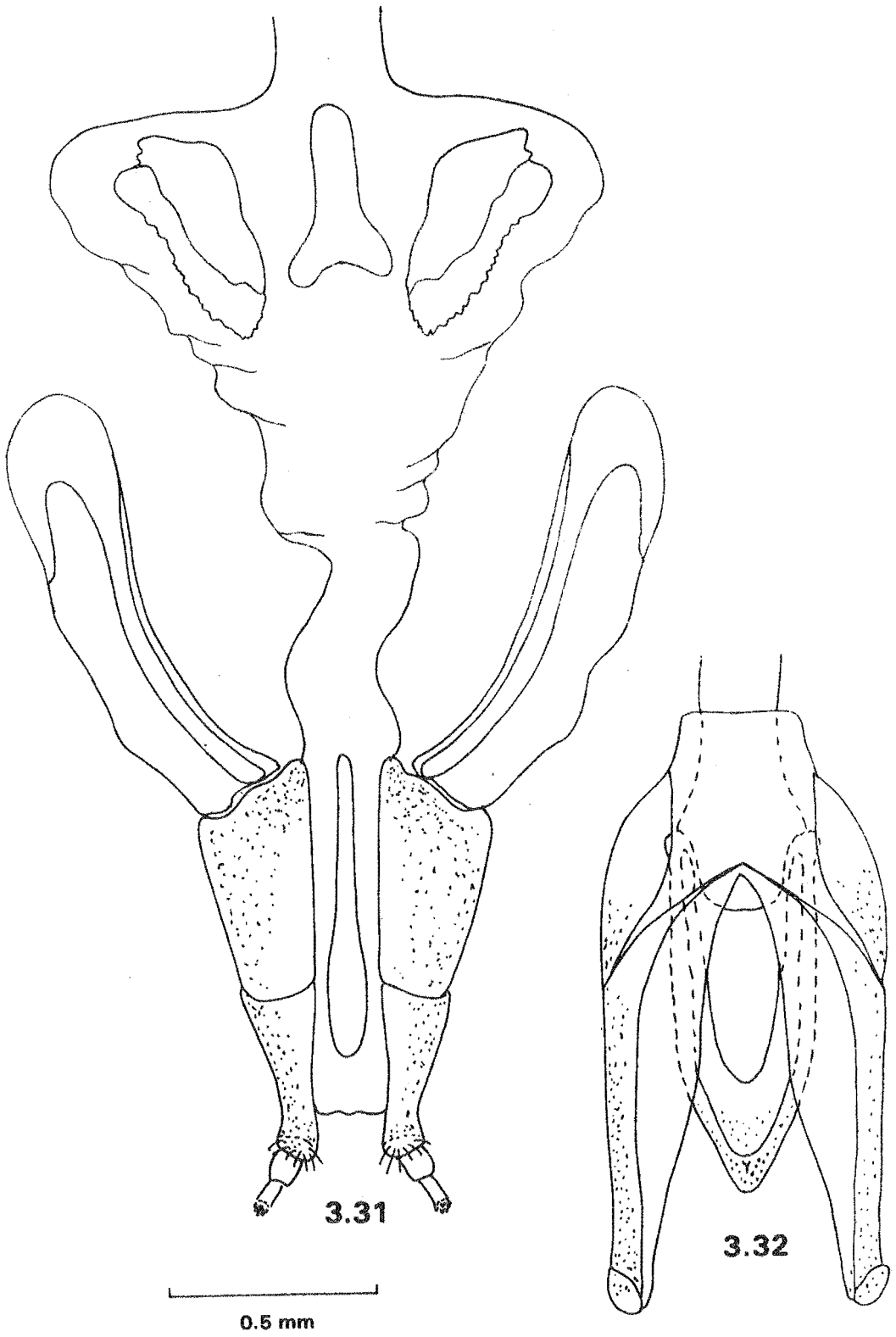


FIGURE 3.30 *Sclerocyphon aquaticus*, ♀ voucher specimen, ventral view. Scale line = 1 mm.



FIGURES 3.31-3.32 *Sclerocyphon aquaticus:* (3.31) ♀, external genitalia, ventral view; (3.32) ♂, external genitalia, ventral view. Scale lines = 0.5 mm.

margins tapering to bluntly rounded apex, ventral sclerite similar but much shorter, narrower.

Last instar larva (Figure 3.33, Pls 3.13-3.15)

Total length 10.8 mm, total width 6.6 mm, length of ninth tergite 1.5 mm, width of ninth tergite 1.8 mm.

General shape - Broadly ovoid, sometimes circular, thoraco-abdominal shield.

Dorsal surface - Medial region dark brown to black, some small yellow patches, pronotum with light patch above each eye. Lateral laminae light brown with yellow patch before edge.

Entire marginal fringe of setae with two bands visible; inner, narrow, regular light brown band; and outer wide band where setae flexible, transparent, tapering to minute point. Overlying this a sparser, irregularly orientated band of dark brown setae, slightly longer than regular fringe. Trailing edge of laminae with fine transparent fringe of setae.

Dense uniform covering of dark, relatively large sclerotised beads overall, darker dense clump of beads at junction of lateral laminae and body, laminae of tergites 6-8 with distinct transverse row of beads.

Pores, visible as shining yellow dots, scattered over entire surface, densest in medial region.

Twelve paired groups of setae in medial region, one group to each side of midline on each thoracic and abdominal segment. Setae long, black, posteriorly directed, projecting from pores in sloping row, each side of midline (forming triangle about midline). Some groups with grey, shining mucous coat over pores as well. Lateral laminae with transverse row of short, thick, black setae, projecting from pores, above posterior margin.

Pronotum with 5 pairs of irregular pits and 4 pairs of circular

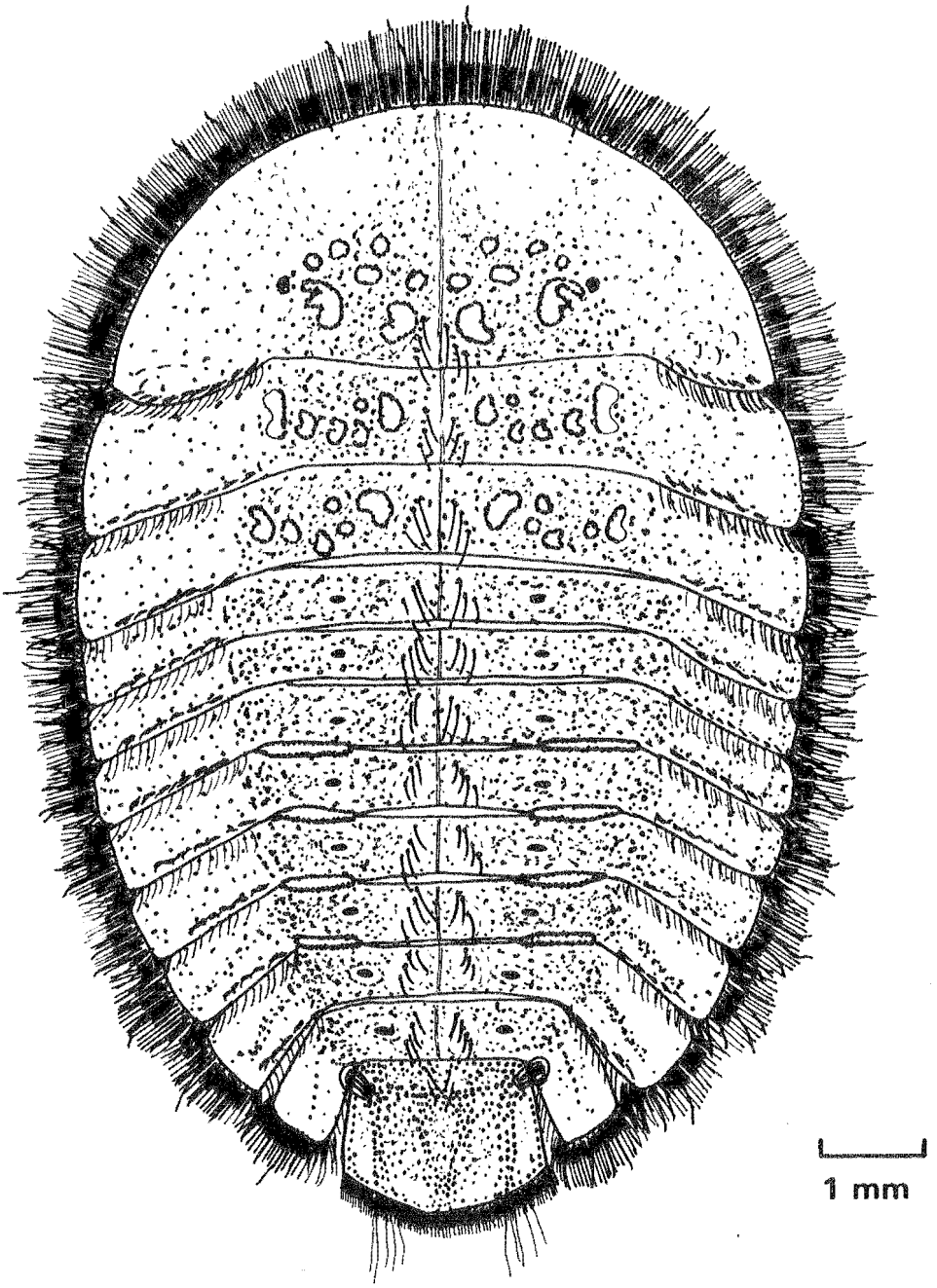
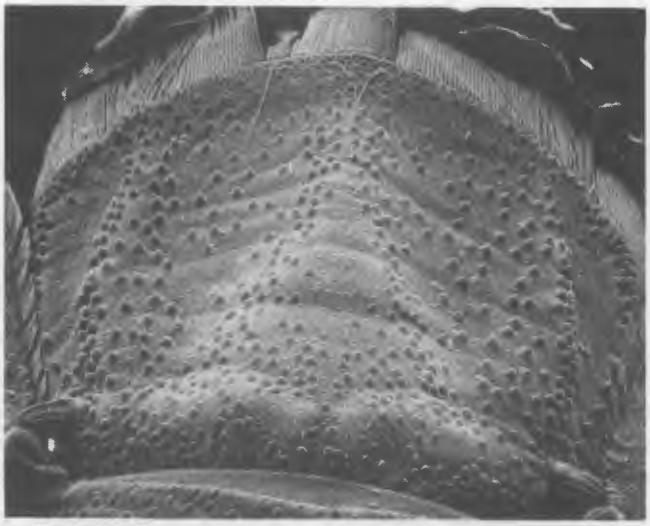
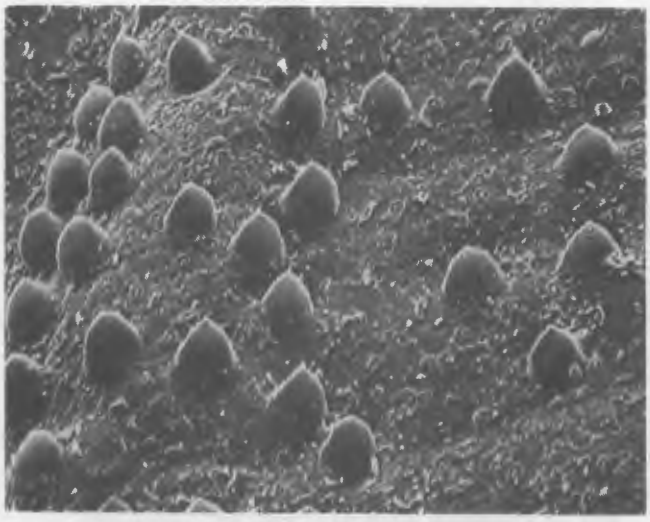


FIGURE 3.33 *Sclerocyphon aquaticus*. last instar larva, voucher specimen, dorsal view. Scale line = 1 mm.

3.13



3.14



3.15

PLATES 3.13-3.15 *Sclerocyphon aquaticus*, last instar larva from Hellyer R, tergite 9: (3.13) x 40; (3.14) x 200; (3.15) x 650.

pits, lateral 3 pairs dark. Meso- and metanotum with 6 pairs of irregular pits. Most pits yellow, all outlined by beads.

Four pairs of gin traps present on adjoining margins of tergites 3-4, 4-5, 5-6 and 6-7, decreasing in width posteriorly.

Tergite 9 (Pls 3.13-3.15) with triangular central upraised region outlined by beads plus a faint lateral ridge, outlined by beads, on each side. Central region often covered with shining mucus. Anterior region densely beaded, beads smaller, sparser posteriorly. Posterior margin weakly produced in a shallow semi-circle, lateral margins straight, sloping. Posterior margin with regular fringe plus group of much longer fine setae each side of middle. Entire tergite nearly square in outline.

Diagnosis

Adults can be distinguished on the following combination of characters; elongate body, "waisted" elytra, shining black derm with irregular ashen pubescence dorsally, and long tapered penile sclerites or elongate vaginal plates.

Larvae can be distinguished on the following combination of characters; 4 gin traps, tergite 9 with shining mucus-coated central triangular upraised region plus two faint lateral ridges and posterior margin produced in shallow semi-circle, ovoid to circular thoraco-abdominal shield with a dense uniform covering of cuticular beads, medial region usually with long black setae projecting from pores each side of midline, lateral laminae with transverse row of short black setae.

Comments

In his description of *S. aquaticus*, Lea (1919) noted that two female paratypes from Hobart (in SAM) differed from the type on several aspects of colour and pubescence and my examination of these specimens

revealed that they are, in fact, *S. secretus* (described subsequently) not *S. aquaticus*. Lea's description, based only on two females from Waratah, could not be considered adequate in the light of present knowledge and thus additions have been given from an examination of voucher specimens.

The larva of *S. aquaticus* is described for the first time here, the larva and adult were associated by laboratory rearing.

S. aquaticus is endemic to Tasmania and occurs throughout most of the State, the distribution of *S. aquaticus* is described in Chapter 4.

Sclerocyphon secretus Smith

(Figures 3.34-3.42, Pls 3.16-3.20)

Sclerocyphon secretus Smith, 1981, p.280

Material Examined

Types - TASMANIA (all Lambert Creek, Sandy Bay, 8312 269491): ♂ holotype (TM Reg. No. F872a, with final larval exuvium F872b and final pupal exuvium F872c); ♀ allotype (TM Reg. No. F873a with final larval exuvium F873b and final pupal exuvium F873c), 1.*x*.1979; paratypes: 1♂ (TM Reg. No. F874, 25.*ix*.1975), 1♂ (TM Reg. No. F875, 19.*xi*.1979, 1♀ (TM Reg. No. F876), 25.*ix*.1975, 1♀ (TM Reg. No. F877), 27.*xi*.1979; larvae, range of instars (TM Reg. No. F878), 5.*xii*.1979; 1♂ (NMV Reg. No. T-6148), 23.*x*.1978, 1♂ (NMV Reg. No. T-6146), 15.*xi*.1979, 1♀ (NMV Reg. No. T-6147), 15.*xi*.1979, larvae (NMV Reg. No. T-6149), 5.*xii*.1979; 1♂, 23.*x*.1978, 1♂, 1♀, 15.*xi*.1979, larvae, 5.*xii*.1979, all in SAM; 1♂, 8.*x*.1978, 1♂, 1♀, 15.*xi*.1979, larvae, 5.*xii*.1979, all in ANIC.

Other non-type material examined - TASMANIA: 14♂♂, 24♀♀, Lambert Ck, 8312 269491, reared in lab., 1975, 1978, 1979; 5♂♂, 4♀♀, Ben Lomond Ck, 8414 538045, reared in lab., *viii-ix*.1978; 18♂♂, 26♀♀, Waterworks Ck, 8312 215485, reared in lab., 1978, 1979; 1♀, Browns R., 8312 206476, 10.*i*.1980; 2♂♂, Dee R., 8213 68112, 1.*xi*.1978; 1♂, 9♀♀, Parsons Bay Ck, 8411 610261, 18.*xi*.1978; 2♂♂, 1♀, Meredith R., 8513 569363, 6.*xiii*.1978; 1♂, Farm Ck, 8014 840819, reared in lab., 17.*vii*.1978. Plus larvae collected from 112 localities (Figure 4.21) (for brevity larval localities are not listed here).

Description

Female (Figure 3.34-3.36)

Total length 5.5 mm, pronotal length 1.0 mm, pronotal width 2.7 mm, elytral length 4.4 mm, elytral width 3.3 mm.

General shape - Oval-elliptic, subconvex beetles.

Pronotum - Dark brown to black, red patches each side of middle. Dense irregular covering of fine ashen pubescence plus denser patches of coarse white pubescence. Medial region convex with median line feebly defined, small shallow transverse impression each side of medial region. Margins narrow, red.

Elytra - Dark brown to black, red patches each side of middle, dense irregular covering of fine ashen pubescence, small dense patches of coarse white pubescence in middle and apical third. Moderately shining derm visible in small glabrous patches. Widest beyond middle, medial region flattened, transverse wrinkles extending laterally from suture in anterior two-thirds. Shallow marginal impression, below shoulder, on each side. Striations obscure.

Thorax - Pro- and mesonotum and antecoxal piece light brown, metanotum black.

Abdomen (Figure 3.35) - Segments 1-4 black laterally and medially, outlined with yellow, remainder light brown. Segment 5 black with light brown medial patch.

External genitalia (Figure 3.36) - Pair of sclerotised hemisternites, punctate, setose distally, bearing 2-segmented styli. Sclerotised rod embedded in ventral vaginal wall between hemisternites not expanded at middle, narrow. Pair of sclerotised plates embedded in anterior dorso-lateral walls of vagina short with pronounced lateral projection.

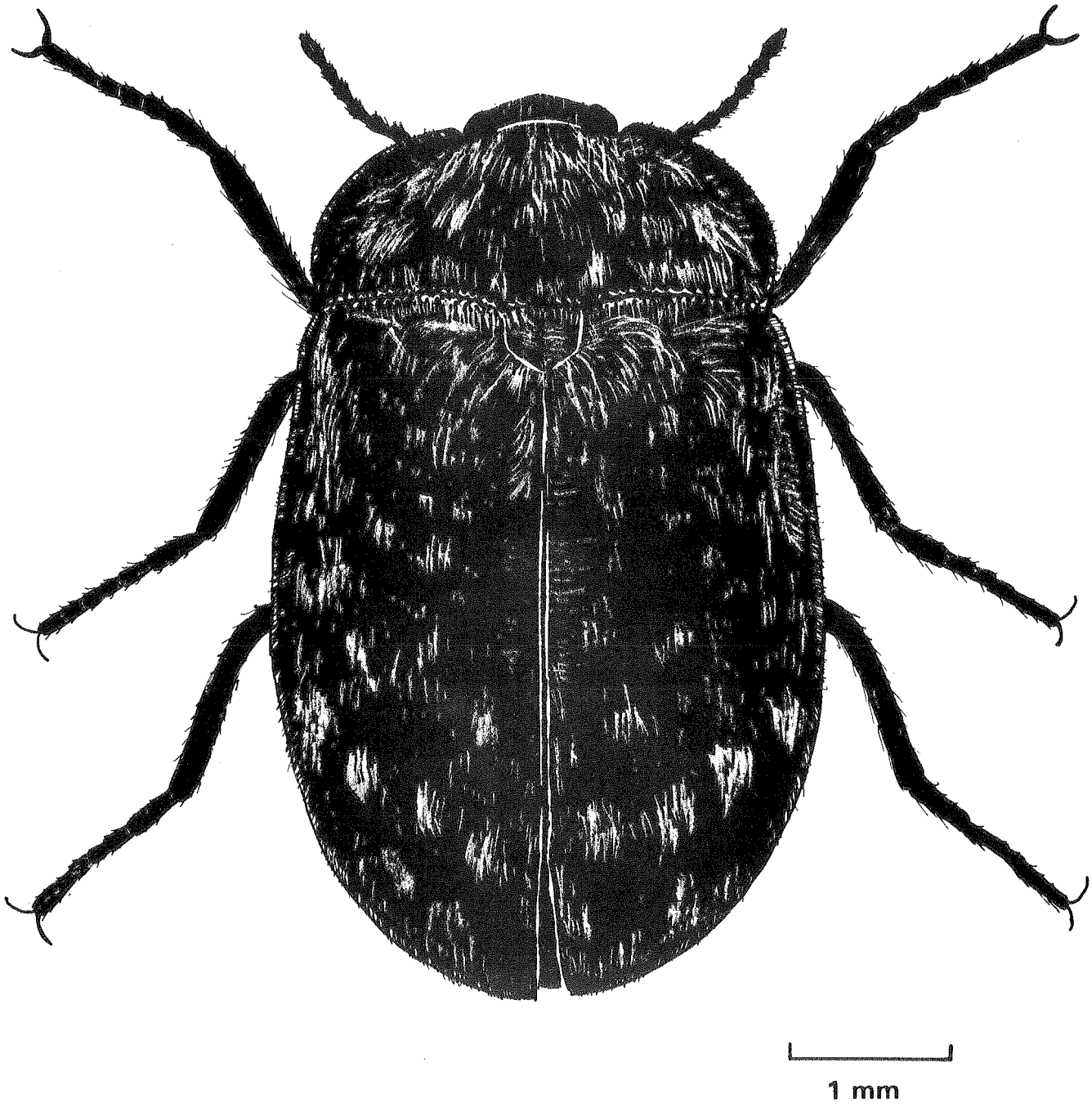


FIGURE 3.34 *Sclerocyphon secretus*, ♀ allotype, dorsal view. Scale line = 1 mm.

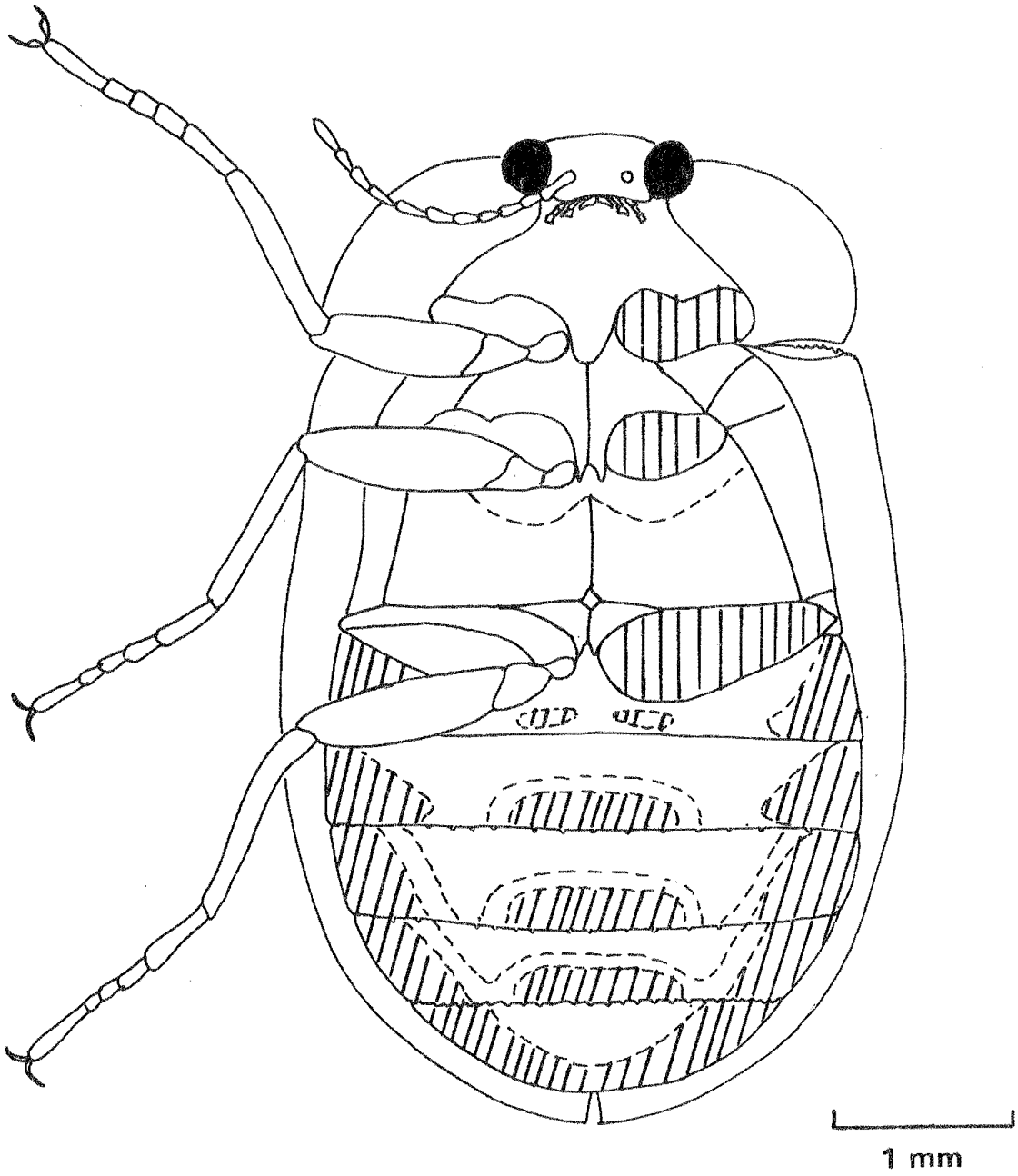
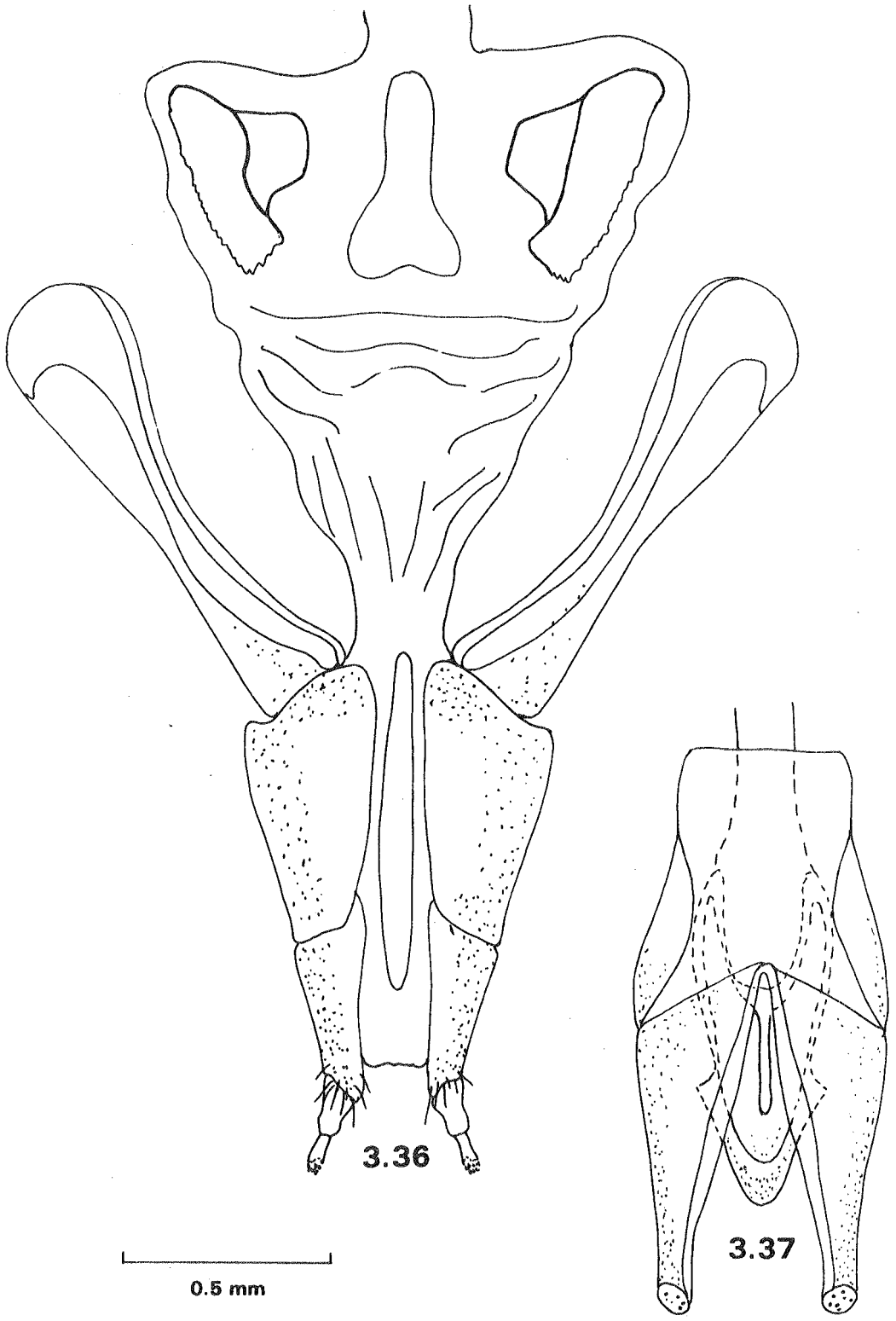


FIGURE 3.35 *Sclerocyphon secretus*, ♀ allotype, ventral view. Scale line = 1 mm.



FIGURES 3.36-3.37 *Sclerocyphon secretus:* (3.36) ♀, external genitalia, ventral view; (3.27) ♂, external genitalia, ventral view. Scale lines = 0.5 mm.

Male (Figure 3.37)

Total length 4.5 mm, pronotal length 0.8 mm, pronotal width 2.2 mm, elytral length 3.5 mm, elytral width 2.7 mm.

Similar to female but smaller.

External genitalia (Figure 3.37) - Aedeagus symmetrical, trilobate. Parameres short, sclerotised with rounded membranous tips. Penis complex, consisting of two sclerites, dorsal sclerite with a sharp projection midway from apex, on each side. Apex rounded. Ventral sclerite small. Lateral margins regularly tapering to rounded apex.

Last instar larva (Figure 3.38, Pls 3.16-3.20)

Total length 7.6 mm, total width 3.6 mm, length of ninth tergite 1.1 mm, width of ninth tergite 1.3 mm.

General shape - Narrow-elliptic thoraco-abdominal shield.

Dorsal surface - Medial region dark brown to black with some yellow patches. Pronotum with yellow patch over eyes. Lateral laminae light brown with yellow patch before edge. Tergite 9 completely dark.

Entire marginal fringe of setae with two bands visible; light brown, regular, inner band and transparent outer band where setae flexible, tapering to minute point. Some setae broken at end of inner band. Trailing edge of laminae with fine transparent fringe.

Covering of dark, sclerotised cuticular beads denser in medial region, sparser on lateral laminae. Tergites 1-8 with two transverse rows of beads across body, darker denser clump of beads at junction of body and lateral laminae. Laminae of tergites 6-8 with transverse row of beads extending across lamina from body to middle.

Pores visible, beneath shining coat of mucus, on transverse upraised strip above ecdysial scar, each side of midline on tergites

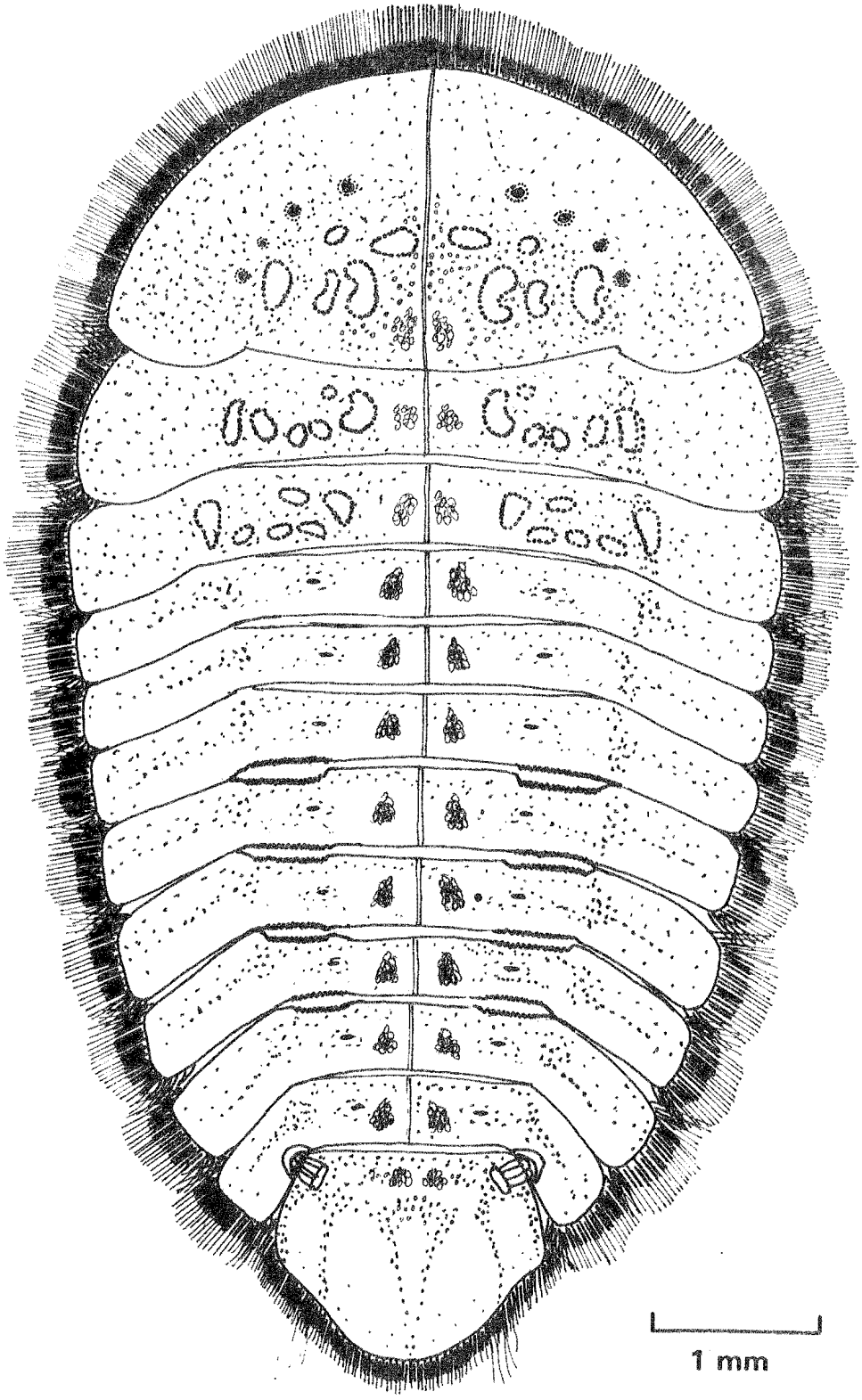
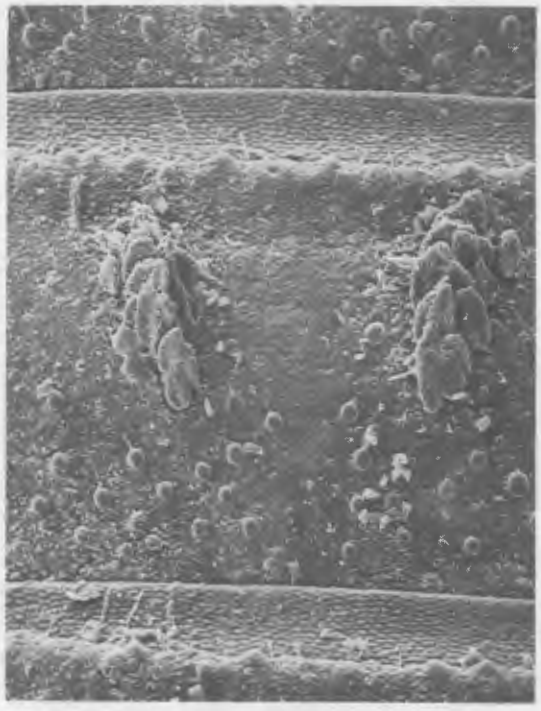
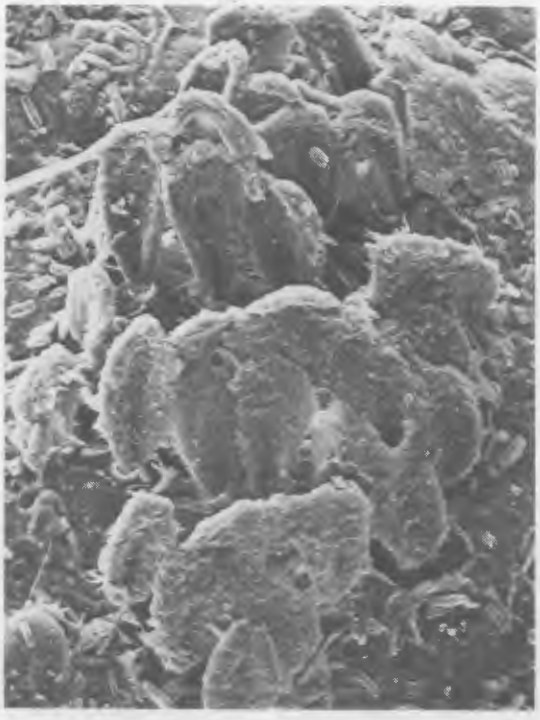


FIGURE 3.38 *Sclerocyphon secretus*, last instar larva, paratype, dorsal view. Scale line = 1 mm.

3.16

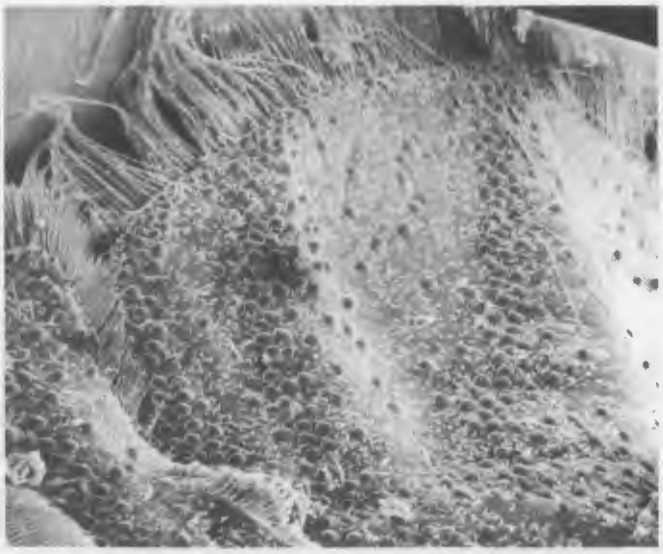


3.17

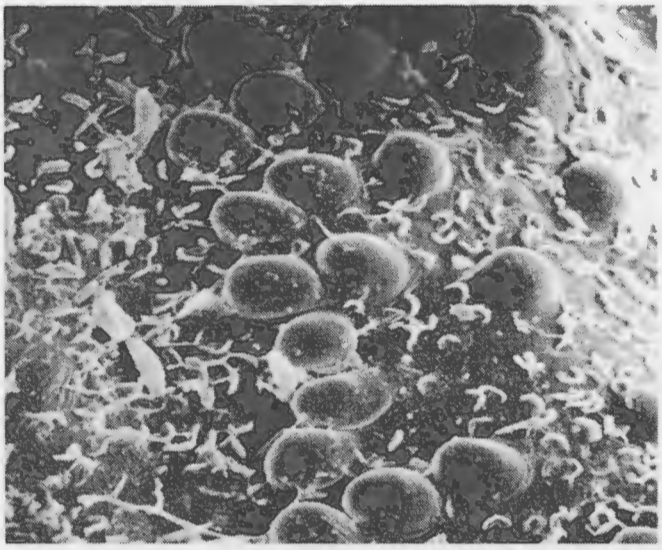


PLATES 3.16-3.17 *Sclerocyphon secretus*, last instar larva from Lambert Ck: (3.16) clumps of mucous-coated trichoid sensilla in mid-dorsal region of tergite 5, x 120; (3.17) clump of mucous-coated trichoid sensilla , x 300.

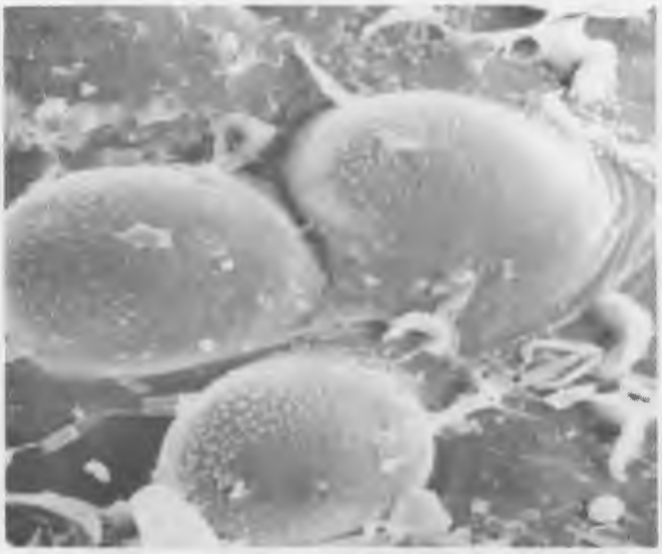
3.18



3.19



3.20



PLATES 3.18-3.20 *Sclerocyphon secretus*, last instar larva from Browns R, tergite 9: (3.18) x 40; (3.19) x 200; (3.20) x 650.

1-8.

Twelve paired groups of trichoid sensilla in medial region. One group to each side of midline on each thoracic and abdominal segment (Pl.3.16). Discrete sensilla visible with scanning electron microscopy (Pl. 3.17). Beneath light microscope sensilla faintly discernible, each group visible as small shining pale mucus-coated mass. Groups on thorax poorly developed.

Pronotum with 5 pairs of irregular pits, 4 pairs of circular pits, all dark coloured. Meso- and metanotum with 6 pairs of irregular pits. Irregular pits nearest midline often dark coloured, remainder light, all bordered by cuticular beads.

Four pairs of gin traps present on adjoining margins of tergites 3-4, 4-5, 5-6 and 6-7. Gin traps decreasing in width posteriorly.

Tergite 9 (Pls 3.18-3.20) with 3 upraised longitudinal ridges, central ridge largest, tapered, extending to posterior margin. All ridges outlined with cuticular beads, beads sparser between ridges and posteriorly. Posterior margin produced in semi-circle medially with rounded or pointed apex, a slight sinuosity present between lateral ridges and apical angles. Lateral margins sloping gently outwards.

Diagnosis

Adults can be distinguished by the following combination of characters; relatively small elongate-oval body, densely pubescent dorsal surface and two well-defined lateral projections, or barbs, on the dorsal penile sclerite or marked lateral projections on the vaginal plates.

Larvae can be distinguished by the following combination of characters; 4 gin traps, tergite 9 with 3 upraised longitudinal ridges, central ridge largest, tapering to posterior margin, posterior margin

produced in semi-circle medially with round or pointed apex, a slight sinuosity each side of middle, lateral margins sloping gently outwards, small mucus-coated clumps of sensilla , and sparser covering of beads on lateral laminae.

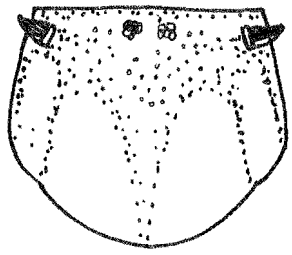
Comments

Adults of *S. secretus* are unique within the genus *Sclerocyphon* in the possession of two lateral projections or barbs on the dorsal penile sclerite of the male and apparently corresponding lateral projections on the vaginal plates of the female. Reasons as to why such distinctive features of the genitalia should be present in *S. secretus* but not in other species of *Sclerocyphon* are discussed in Section 3.5.

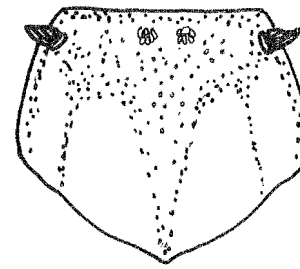
S. secretus is endemic to Tasmania and is the most common and widespread species of *Sclerocyphon* in Tasmania. The distribution of *S. secretus* is given in Chapter 4.

Some variation is present in the larval form of *S. secretus*. Generally larval colour varies according to substrate. Pale, semi-transparent larvae occur on light-coloured stones, in particular, on the quartzitic substrates of many streams in the south-west of Tasmania. Darker larvae occur on the darker substrates, in particular, on dolerite substrates. Some larvae exhibit disruptive colour patterns with alternating regions of light and dark coloration.

The shape of the ninth tergite can vary from the rounded form typical of the type locality, Lambert Creek (Figure 3.39) to a more pointed form (3.40) common in the Ben Lomond Creek population in northern Tasmania. The shape of the thoraco-abdominal shield can vary from narrow and elongate (Figure 3.41) to wide and ovoid (Figure 3.42). A detailed analysis of larval shape in *S. secretus* is described in Chapter 5. Adults reared from larvae exhibiting variation in the ninth tergite and the shape of the dorsal shield

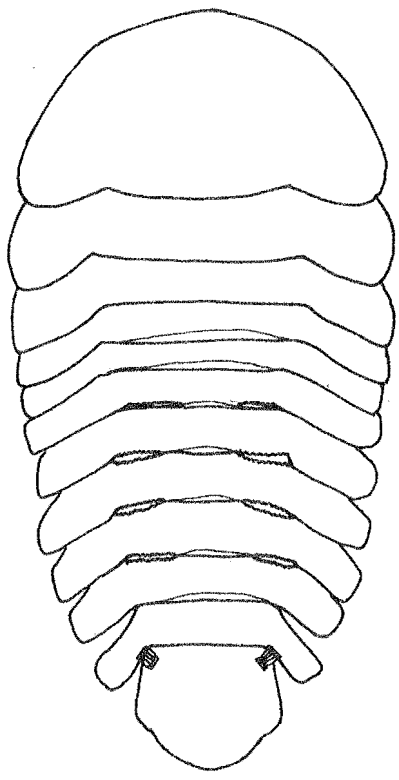


3.39

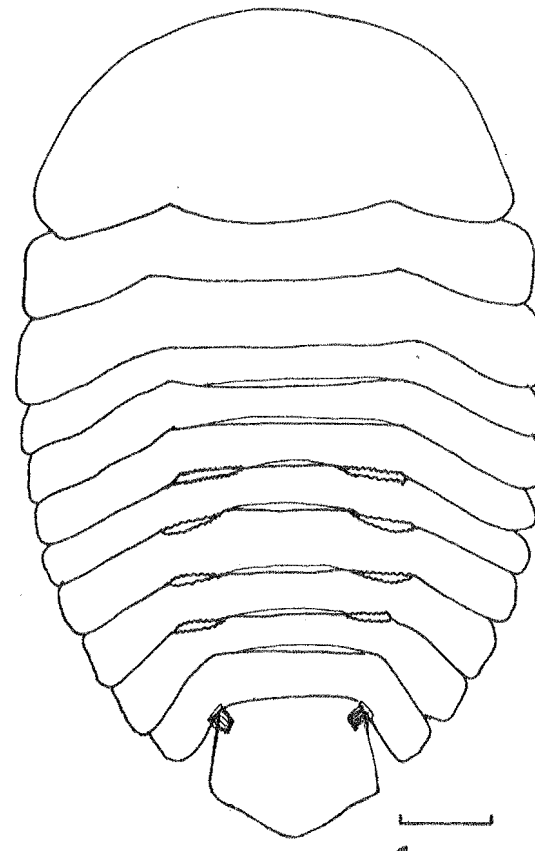


3.40

1 mm



3.41



1 mm

3.42

FIGURES 3.39-3.42 *Sclerocyphon secretus*, last instar larva: (3.39) tergite 9 of larva from Lambert Ck, dorsal view; (3.40) tergite 9 of larva from Ben Lomond Ck, dorsal view; (3.41) thoraco-abdominal shield of larva from Lambert Ck, dorsal view; (3.42) thoraco-abdominal shield of larva from Browns R, dorsal view. Scale lines = 1 mm.

were all clearly identifiable as *S. secretus*.

The specific epithet was chosen to denote the secretive habit of both adults and larvae.

Sclerocyphon aquilonius sp.n.

(Figures 3.43-3.46)

Material Examined

Types - QUEENSLAND: (all Crystal Cascades via Cairns) holotype ♀ QM Reg. No. 8469, 6.*xii*.1966, B. Cantrell, (QU), QM; allotype ♂, 30.*xii*.1963, G. Monteith, QU.

Description

Female (Figures 3.43-3.45)

Total length 6.65 mm, head width 1.25 mm, pronotal length 1.45 mm, pronotal width 3.8 mm, width between apical angles of pronotum 1.75 mm, scutellar length 0.45 mm, scutellar width 0.65 mm, elytral length 5.1 mm, elytral width 4.55 mm.

General shape - Widely ovoid, sub-convex beetle.

Head - Brown.

Pronotum - Uniformly dark brown, dense coarse pubescence overall except glabrous, shining region in middle, above scutellum and some small glabrous patches across base. Medial region gently convex, sloping to very wide, flattened lateral margins. Apical angles shallow, blunt. Lateral margins yellow.

Scutellum - Brown.

Elytra - Dark brown laterally and apically, region adjoining scutellum and elytral suture (to middle) yellow with brown patches. Fine dark pubescence over most of elytra, dark shining region of derm, either side of suture, below middle, bordered by large patches of coarse white pubescence. Smaller patches of coarse white pubescence scattered over rest of elytra. Striations visible laterally, marked by longitudinal rows of white pubescence. Medial region

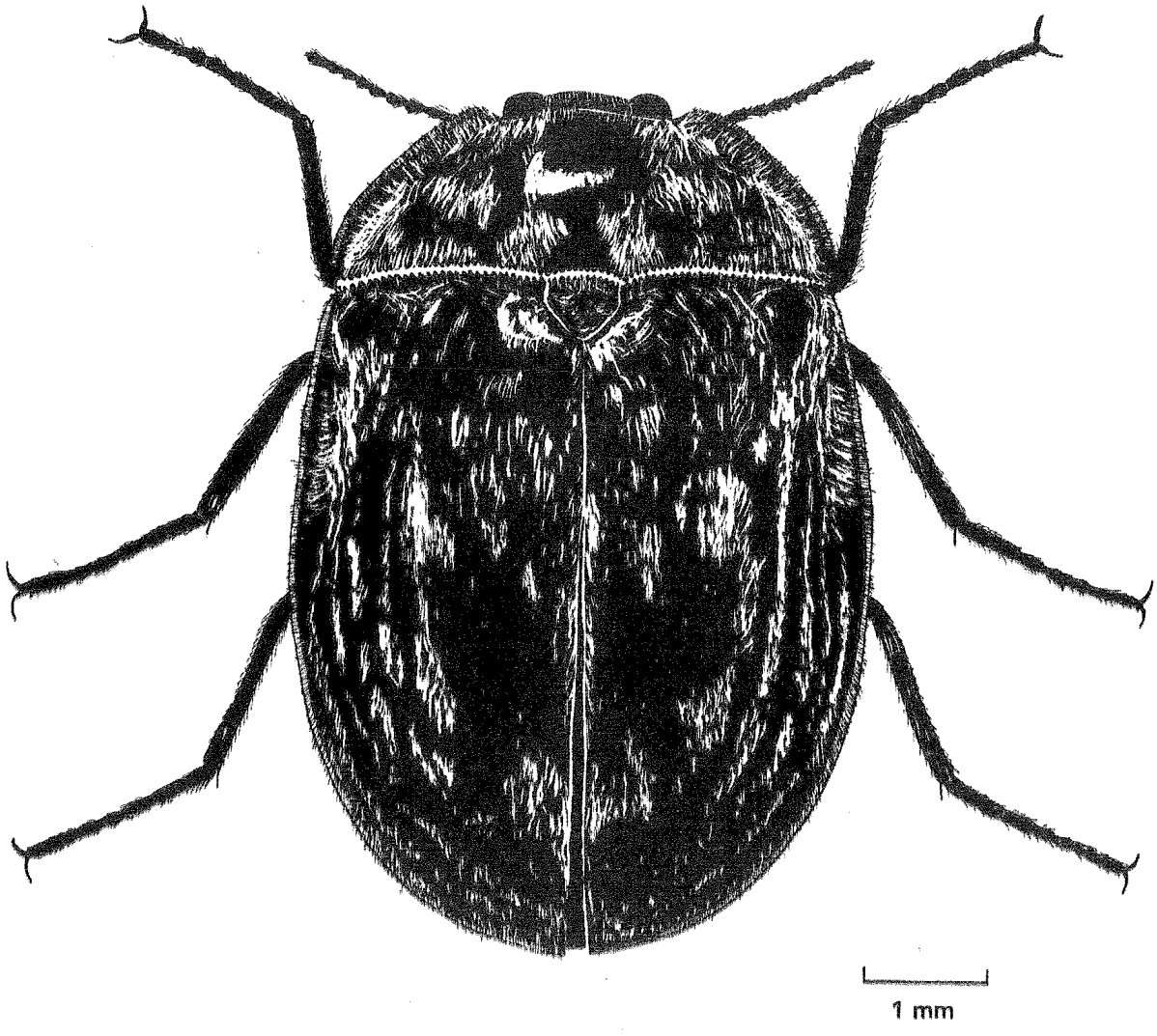


FIGURE 3.43 *Sclerocyphon aquilonius*, ♀, holotype, dorsal view. Scale line = 1 mm.

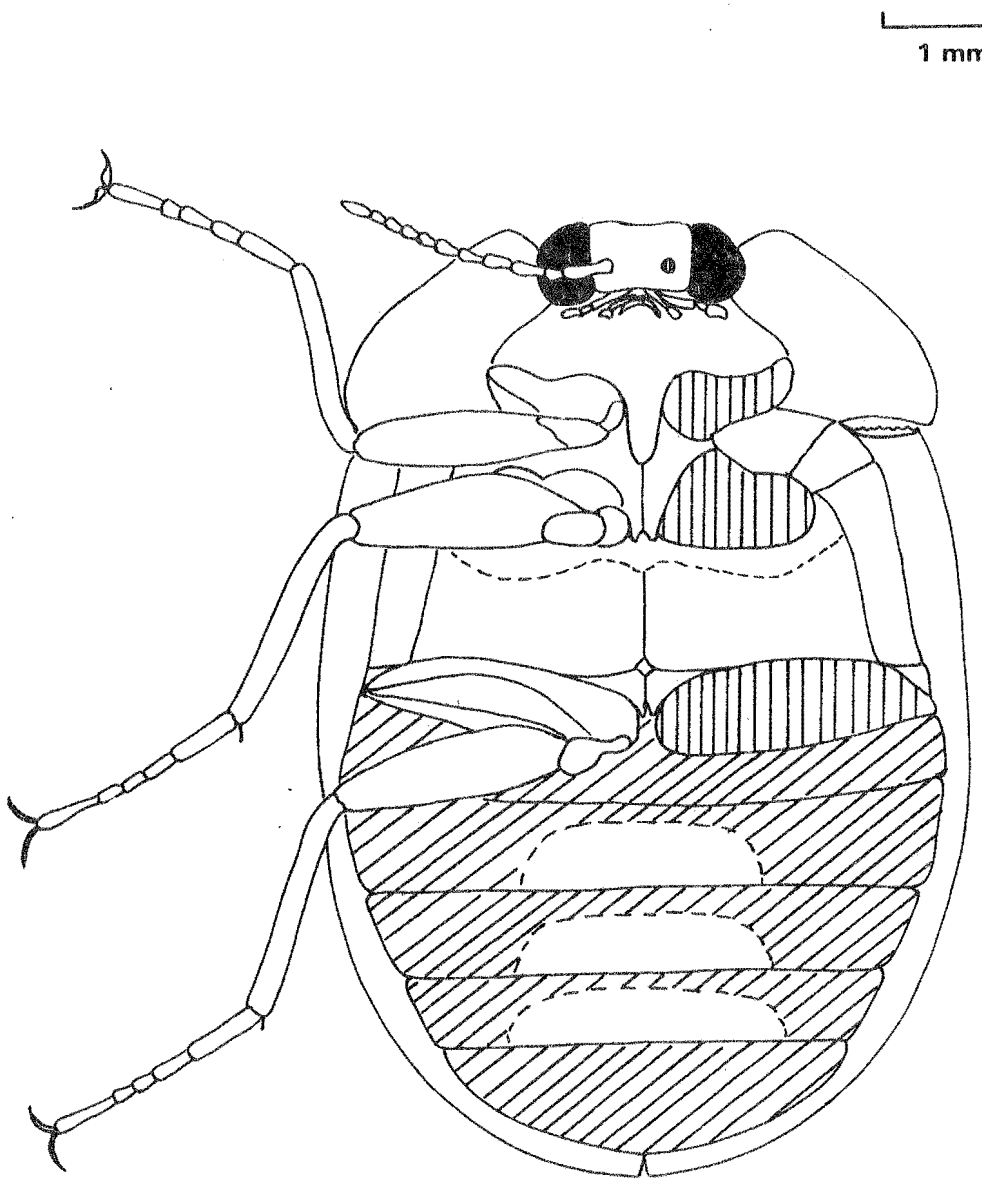
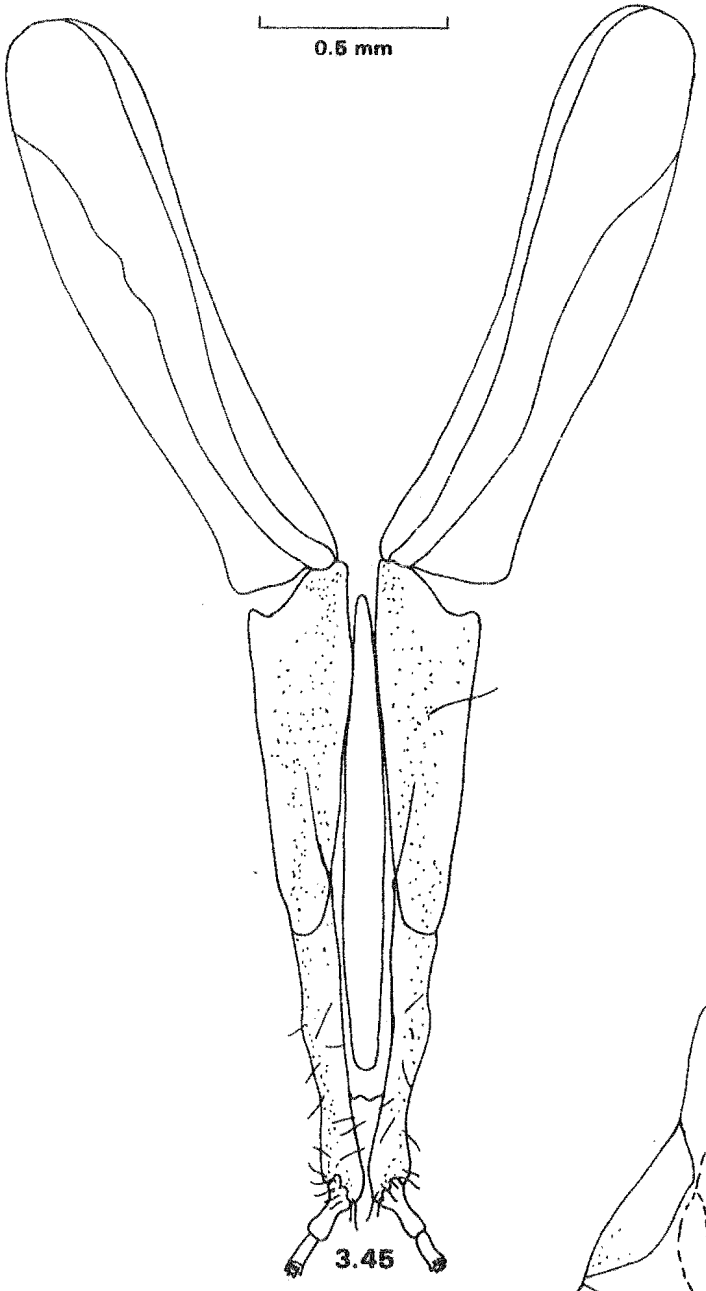
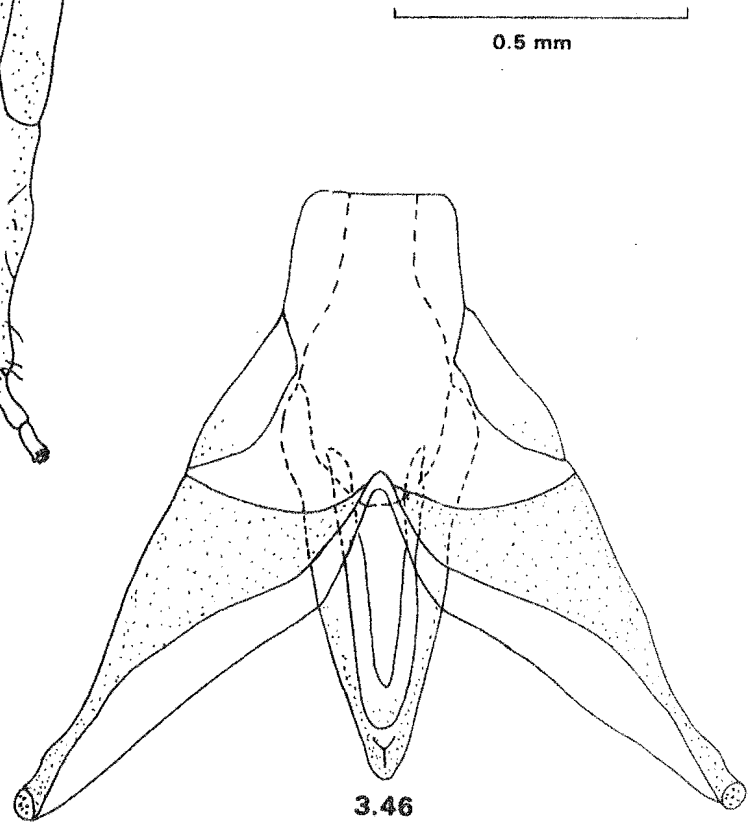


FIGURE 3.44 *Sclerocyphon aquilonius*, ♀, ventral view. Scale line = 1 mm.





FIGURES 3.45-3.46 *Sclerocyphon aquilonius:* (3.45) ♀, holotype, external genitalia, ventral view; (3.46) ♂, external genitalia, ventral view. Scale lines = 0.5 mm.

flattened, derm shiny, transverse wrinkles extending from scutellum. Very wide, shallow marginal impression, each side, below glabrous shoulder. Elytra widest beyond middle. Margins very wide, yellow.

Legs - Femur, tibia and tarsi all light brown.

Thorax - Pro-, meso- and metasternum yellow.

Abdomen (Figure 3.44) - Abdomen predominantly brown, segments 2, 3 and 4 with yellow patches medially.

External genitalia (Figure 3.45) - Pair of long, narrow, sclerotised hemisternites, setose in distal half, punctate, bearing 2-segmented styli. Sclerotised rod embedded in vaginal wall between hemisternites, long, narrow, broader posteriorly. Vaginal plates missing, probably lost in preparation of slide.

Male (Figure 3.46)

Total length 5.8 mm, head width 1.25 mm, pronotal length 1.3 mm, pronotal width 3.5 mm, width between apical angles of pronotum 1.6 mm, scutellar length 0.45 mm, scutellar width 0.6 mm, elytral length 4.4 mm, elytral width 4.05 mm.

Similar to female but smaller, pronotum and elytra more densely covered with coarse white pubescence.

Abdomen - Segment 3 with pubescence parted at midline, posterior margin produced posteriorly each side of midline.

External genitalia (Figure 3.46) - Aedeagus symmetrical, trilobate. Parameres long, sclerotised, punctate, tapering to membranous tips. Penis complex, consisting of two sclerites, dorsal sclerite long, lateral margins tapering to narrow, rounded apex, ventral sclerite similar but much shorter, narrower.

Diagnosis

Adults can be distinguished on the following combination of

characters; relatively large size, broad, flattened, widely e-marginate elytra, elytral striations with longitudinal rows of white pubescence, and long, narrow form of both male and female genitalia (Figures 3.45, 3.46).

Comments

Only two specimens, one female and one male (subsequently designated holotype and allotype) of this species are known; however, their distinctive morphology warranted their description as a new species.

The two specimens were present within a larger sample of *S. minimus* sp.nov. from Crystal Cascades, near Cairns, north Queensland. The specific epithet, meaning northern, was chosen to illustrate the species apparently restricted northern distribution.

As yet no adult-larva association has been obtained. *S.* type A (described below) may be the larva of this species, by virtue of its similarly restricted north Queensland distribution and very broad larval form. Further collection and laboratory rearing of this species is now required.

Sclerocyphon armstrongi sp.n.

(Figures 3.47-3.51, Pls 3.21-3.24)

Material Examined

Types - SOUTH AUSTRALIA: holotype ♀ (in spirit with pupal exuvium, genitalia dissected, in smaller vial), Dry Creek, Valley View, Adelaide, Aug.1963, C. Watts, SAM; allotype ♂, same data as holotype, SAM. Paratypes: 5 L, Torrens R, 500 m downstream of Torrens Gorge weir, 7.*i*.1980, J. Ferris, SAM; 5 L, same data as preceding sample, NMV.

Other material examined - SOUTH AUSTRALIA: 1♀, 1♂, Adelaide, C. Watts; 1 ♀ with pupal and larval exuviae, 1♂, Torrens R., 500 m downstream of Torrens Gorge weir, 7.*i*.1980, J. Ferris, emerged in lab., 1980; 1♀, 1♂, 4 Pe, 24 L (7.*i*.1980), 4 L (12.*vi*.1978), 14 L (Jan.1981, Torrens R., 500 m downstream of Torrens Gorge weir, J. Ferris; 3 L, 1 Pe, Deep Ck, Montacute, 18.*i*.1979, H.B.N. Hynes; 2 L, Trib. of Deep Ck, at ford, 11.*xi*.1975, J.E. Bishop, WDW; 3 L, Deep Ck, 0.5 mi from Castanbul, 11.*xi*.1975, J.E. Bishop, WDW; 10 L, Deep Ck ford, 3.*iv*.1975, 1.*x*.1976, J.E. Bishop, WDW; 9 L, Trib. of Deep Ck, Castanbul, 4.*iii*. 1977, J.E. Bishop, WDW; 6 L, Deep Ck, 10.*v*.1976, 28.*x*.1976, J.E. Bishop, WDW; 3 L, Deep Ck, 1.*vi*.1976, P. Suter, WDW; 3 L, Little Para R., 1.*iv*.1976, J.E. Bishop, WDW; 5 L, Brownhill Ck Ford, 20.*iii*.1975, J.E. Bishop, WDW; 9 L, Kangarilla Ck on Meadows Rd, 21.*x*.1976, J.E. Bishop, WDW; 4 L, Sturt R. at Bedford Park, 27.*viii*. 1976, J.E. Bishop, WDW; 4 L, Tenafeate Ck, Mt. Lofty Ra., Aug.1978, P. Harrison, WDW. VICTORIA: 1 ♀ (labelled: "*Sclerocyphon fuscus* Armstrong, identified J. Armstrong, holotype") Clarendon, C.J. Hackett, SAM; 1 ♀, Pe, Le, 1♀, 2♂, Mt. Emu Ck, Jan.1959, CW; 2 L, Grampians, Feb.1955, CW.

Description

Female (Figures 3.47-3.49)

Total length 5.45 mm, head width 1.05 mm, pronotal length 1.2 mm, pronotal width 2.9 mm, width between apical angles of pronotum 1.3 mm, scutellar length 0.4 mm, scutellar width 0.6 mm, elytral length 4.2 mm, elytral width 3.45 mm.

General shape - Elliptic, subconvex beetles.

Head - Brown.

Pronotum - Brown, dense coarse ashen pubescence, sparse in medial region, derm, where visible, punctate, moderately shiny. Six dense patches of coarse pubescence across basal region. Margins yellow, straight laterally, deflexed forwards in anterior region curving around to blunt apical angles.

Scutellum - Inner region dark brown, edges lighter.

Elytra - Dark brown, medial region lighter, elytral suture bordered on each side by narrow, yellow strip. Fine ashen pubescence overall plus small clumps of dense, coarse pubescence in longitudinal rows between striae. Elytra gently convex, medial region flattened, greatest width attained at apical third. Wide shallow transverse marginal impression on lateral margin in basal third. Lateral margins narrow, yellow.

Legs - Femur dark brown, tibia brown, tarsi yellow.

Thorax - Pro- and mesosternum yellow, metasternum dark brown, antecoxal piece yellow, remainder dark brown.

Abdomen (Figure 3.48) - Segments 1-5 with dark brown/light brown colour pattern, narrowly outlined with yellow.

External genitalia (Figure 3.49) - Pair of sclerotised hemisternites punctate, setose distally, bearing 2-segmented styli.

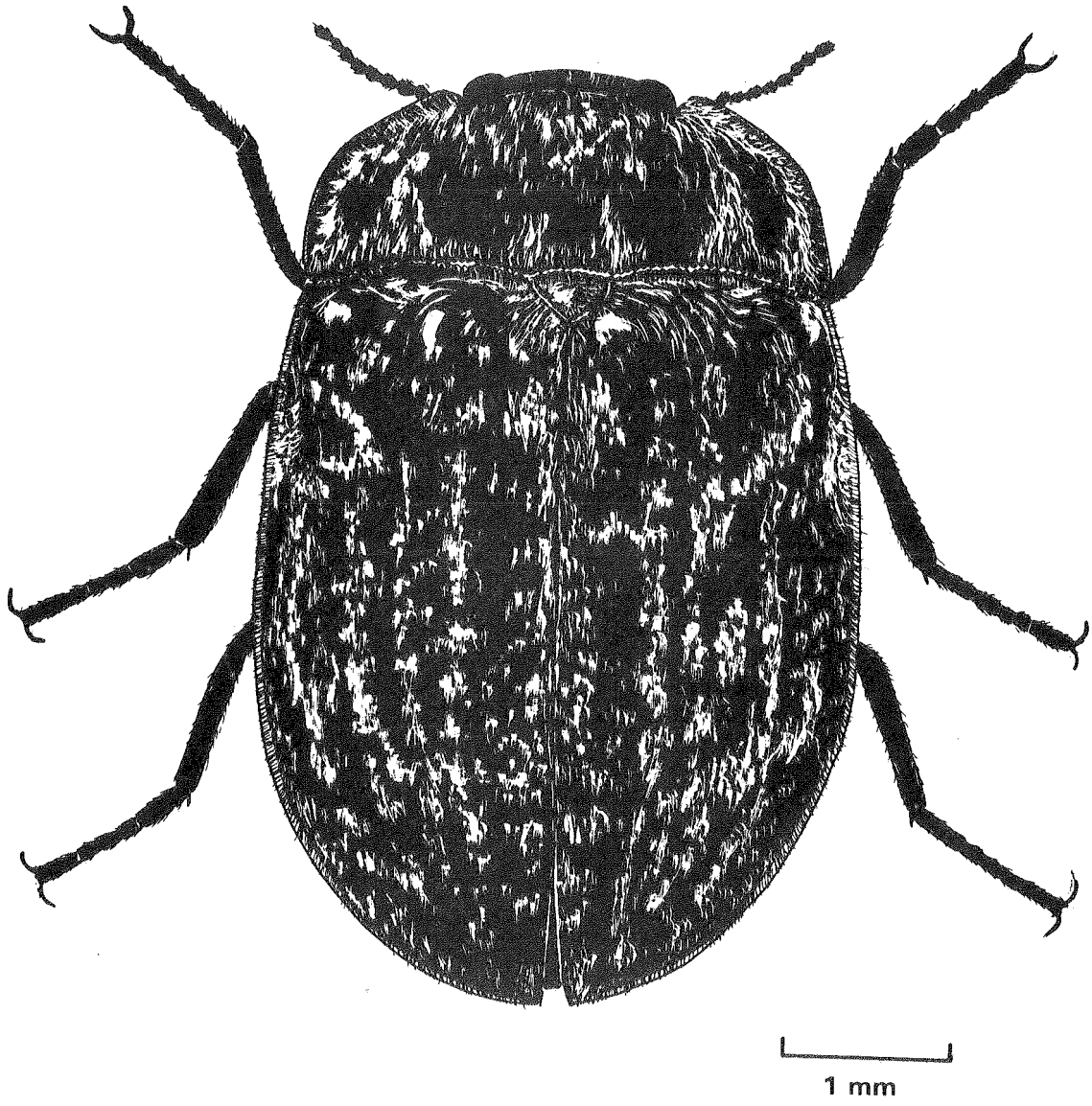


FIGURE 3.47 *Sclerocyphon armstrongi*, ♀, holotype, dorsal view. Scale line = 1 mm.

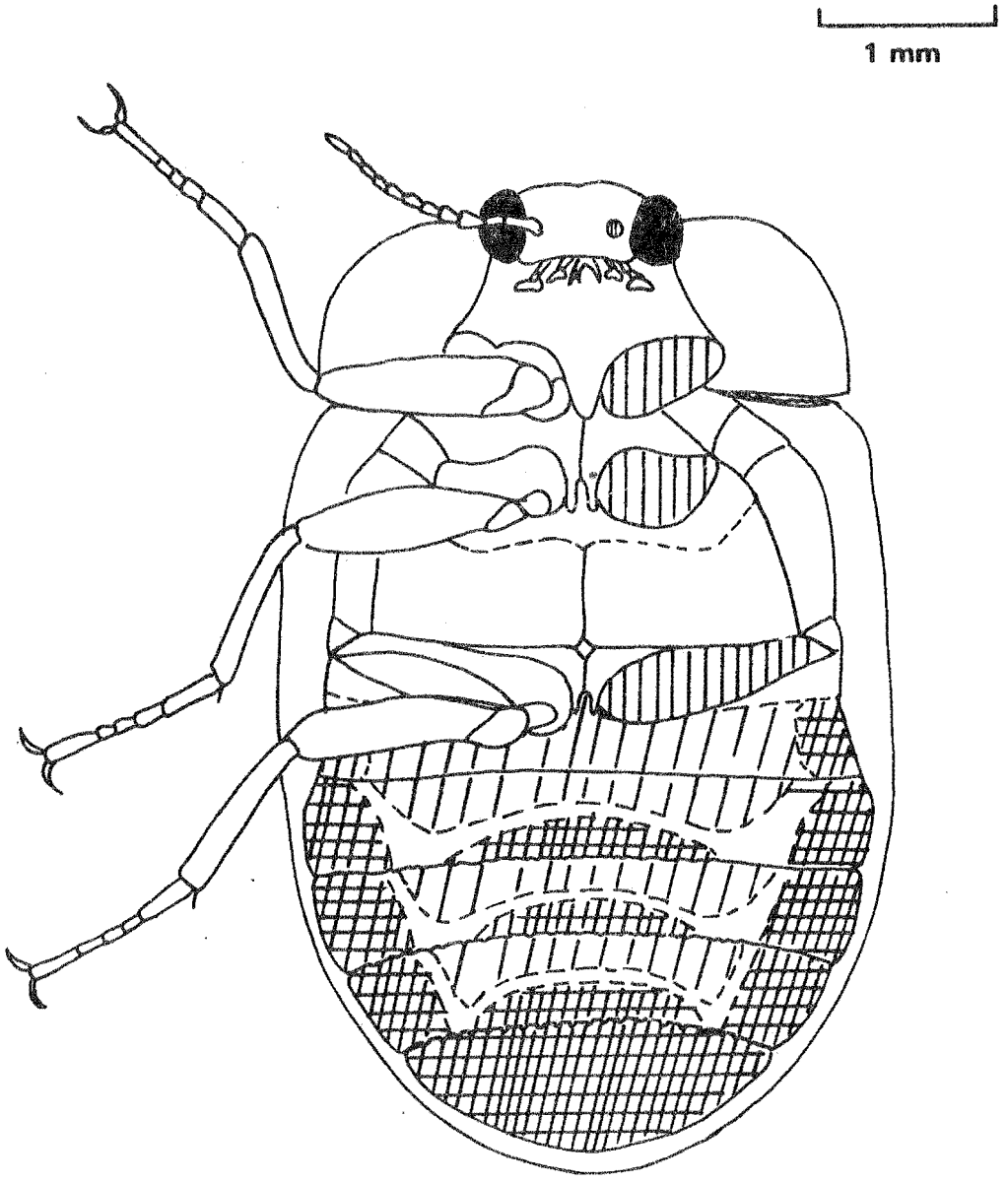
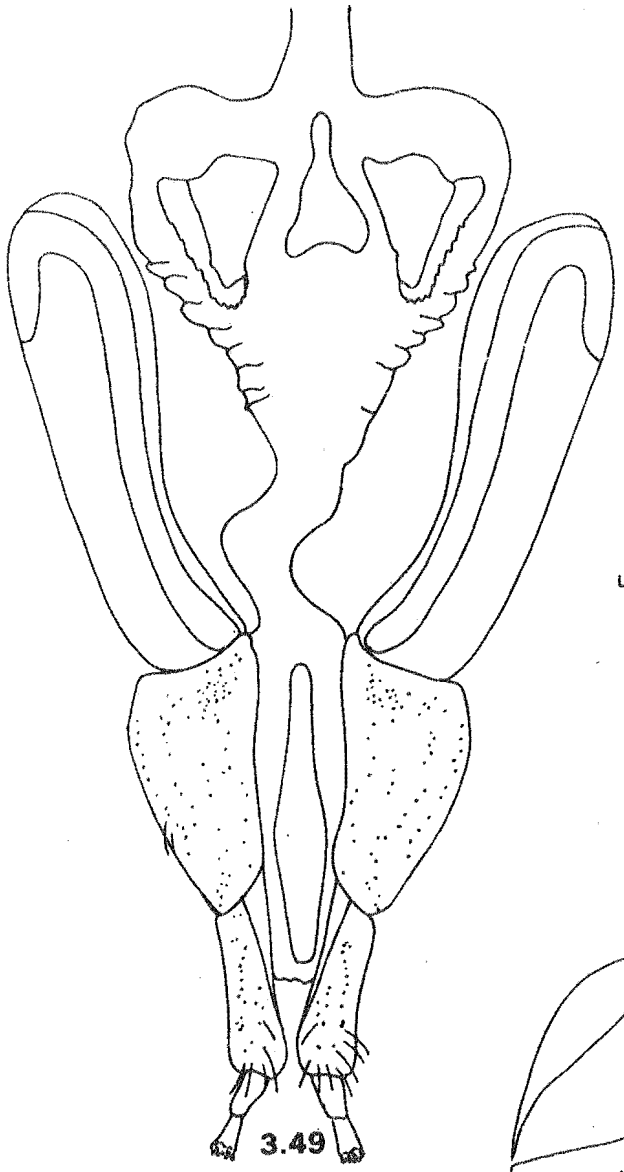
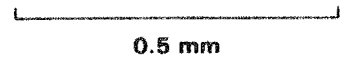
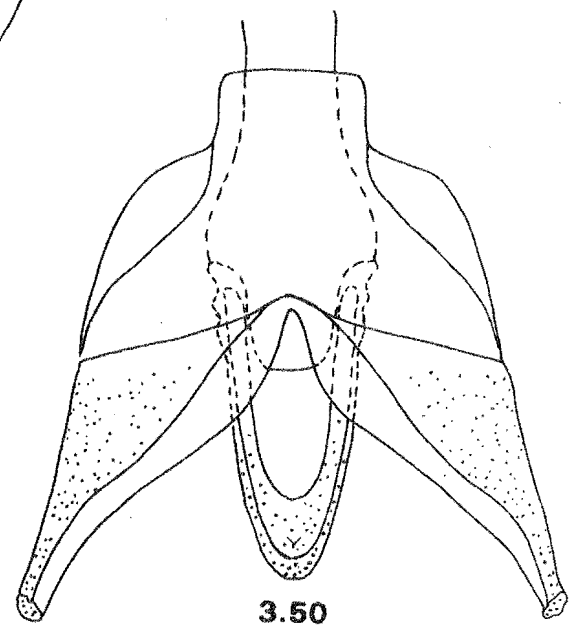


FIGURE 3.48 *Sclerocyphon armstrongi*, ♀, holotype, dorsal view. Scale line = 1 mm.







FIGURES 3.49-3.50 *Sclerocyphon armstrongi:* (3.49) ♀ external genitalia, ventral view; (3.50) ♂ external genitalia, ventral view. Scale lines = 0.5 mm.

Sclerotised rod, embedded in vaginal wall between hemisternites, expanded medially, broader posteriorly than anteriorly. Pair of sclerotised plates, embedded in anterior dorso-lateral vaginal walls, broad anteriorly, tapering to narrow apex posteriorly.

Male (Figure 3.50)

Total length 4.25 mm, head width 0.9 mm, pronotal length 0.95 mm, pronotal width 2.3 mm, width between apical angles of pronotum 1.1 mm, scutellar length 0.35 mm, scutellar width 0.4 mm, elytral length 3.25 mm, elytral width 2.7 mm.

Similar to female but smaller.

Elytra - Patches of pubescence less regular than female, anterior medial region relatively glabrous, transverse wrinkles extending from suture visible.

External genitalia (Figure 3.50) - Aedeagus symmetrical, trilobate. Parameres sclerotised, punctate, narrowing to membranous tips. Penis complex, consisting of two sclerites, dorsal sclerite narrow, lateral margins tapering to rounded apex, ventral sclerite similar, smaller.

Last instar larva (Figure 3.51, Pls 3.21-3.24)

Total length 8.9 mm, total width 4.8 mm, length of ninth tergite 1.2 mm, width of ninth tergite 1.6 mm.

General shape - Narrow elongate thoraco-abdominal shield, widest at tergite 1, tapering to tergite 9.

Dorsal surface - Medial region brown, tergites 1, 2 and 6 with pair of yellow patches, tergites 3, 4, 5, 7 and 8 with dark brown patches. Pronotum with light region above each eye, dark brown over head. Lateral laminae lighter, 3 alternating regions of colour: yellow, brown, yellow. Tergite 9 dark brown with yellow Y-shaped patch at centre of base.

Entire marginal fringe of setae with two bands visible; narrow,

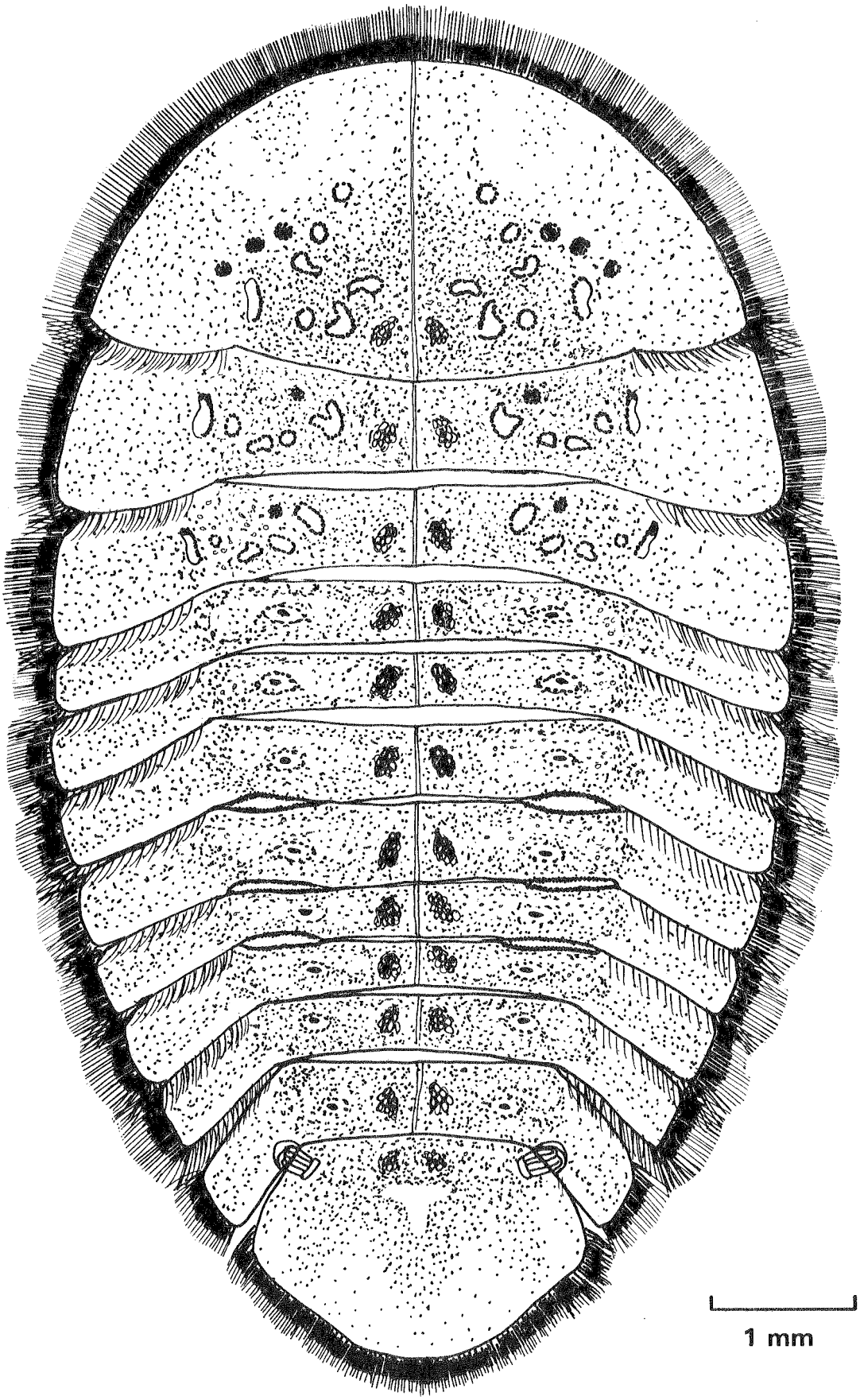
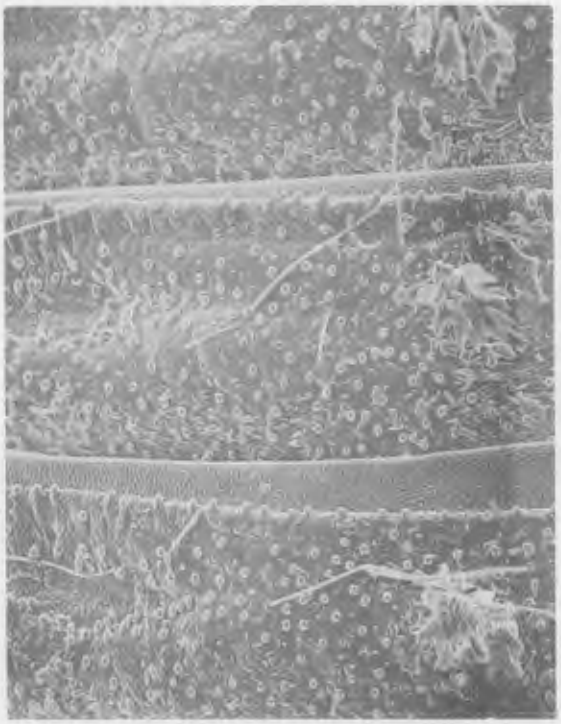
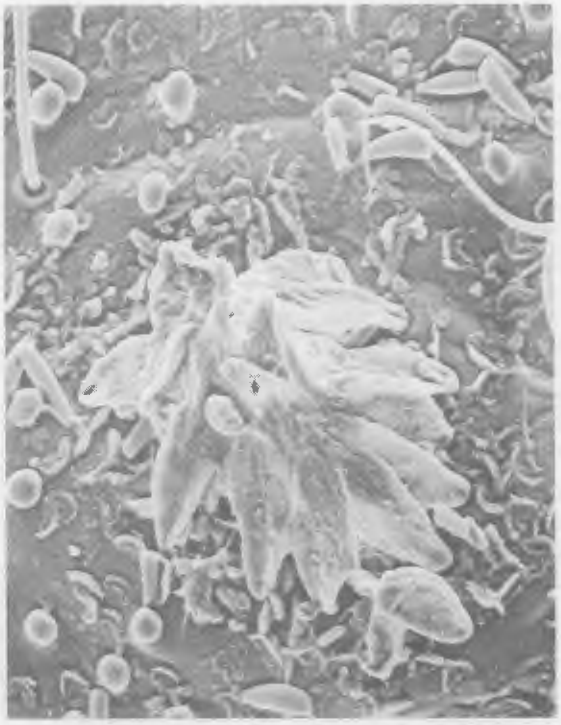


FIGURE 3.51 *Sclerocyphon armstrongi*, last instar larva, paratype, dorsal view. Scale line = 1 mm.



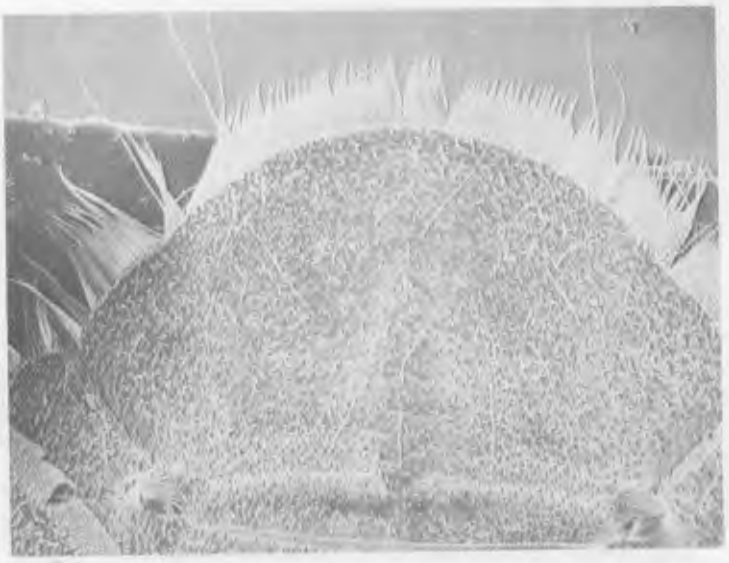
3.21



3.22

PLATES 3.21-3.22 *Sclerocyphon armstrongi*, last instar larva from Torrens R: (3.21) clumps of mucous-coated trichoid sensilla in mid-dorsal region of tergites 5, 6 and 7, x 100; (3.22) clump of mucous-coated trichoid sensilla , x 400.

3.23



3.24

PLATES 3.23-3.24 *Sclerocyphon armstrongi*, last instar larva from Torrens R, tergite 9: (3.23) x 40; (3.24) x 650.

light brown inner section, wide transparent outer section. Some setae brown for entire length. Trailing edge of all laminae with fringe of fine transparent setae.

Dense, uniform covering of sclerotised, pointed,cuticular beads over entire dorsal surface except for bare narrow strip along posterior margin of lateral laminae of tergites 1-8. Dark, denser clump of beads at junction of laminae and abdomen on tergites 1-8.

Pores, visible as shining yellow dots, scattered throughout medial region, smaller on lateral laminae. Two denser regions of pores on each side of ecdysial scar, each side of midline, on tergites 1-8, some with grey shining coat of mucus, some with fine hairs protruding from pores.

Twelve paired groups of trichoid sensilla in medial region, one group to each side of midline on each thoracic and abdominal segment. Discrete sensilla visible only with scanning electron microscopy (Pls 3.21, 3.22). Beneath light microscope each group visible as shining, grey, elliptic, mucus-coated mass. Largest groups on tergites 1-4.

Pronotum with 5 pairs of irregular pits, 4 pairs of circular pits, lateral 3 dark, and one pair of pits anteriorly. Meso- and metanotum with 6 pairs of irregular pits, second pit from midline, on each side, dark. All other pits light-coloured.

Three pairs of gin traps present on adjoining margins of tergites 3-4, 4-5 and 5-6, all pairs similar width.

Tergite 9 (Pls 3.23, 3.24) without distinct ridges, base with light, shining mucus-coated Y-shaped region, highest at anterior margin, sloping to posterior margin. Cuticular beads densest at base, sparser near posterior margin. Posterior margin produced in a regular semi-circle medially, bordered on each side by concave sinuosity, apical angles rounded, lateral margins curved. Broadly triangular outline overall.

Diagnosis

Adults can be distinguished by the following combination of characters; elliptic subconvex body (neither as elongate as *S. striatus* nor as broad as *S. zwicki*), nearly entire covering of ashen pubescence with small white clumps in longitudinal rows between striae, moderately shining dorsal surface, and narrow elongate penile sclerites or anteriorly widened vaginal plates.

Larvae can be distinguished by the following combination of characters: 3 gin traps, the form of tergite 9 with its broadly triangular outline, posterior margin produced in regular semi-circle bordered each side by concave sinuosity, and lack of upraised ridges, and elliptic medial clumps of trichoid sensilla .

Comments

Despite the fact that a specimen of this species, labelled "*Sclerocyphon fuscus* Armstrong, holotype", is held in the South Australian Museum, no formal description of *S. fuscus* exists. Bertrand and Watts (1965) mentioned the species "*Sclerocyphon fuscus* Armstrong *in litt.*" in their review of *Sclerocyphon* larvae, thus creating a *nomen nudum*.

The description given here represents the first description of the species, the specific epithet has been chosen to honour J. Armstrong's initial recognition of the species.

Present distribution records indicate that this species is restricted to the south-east of South Australia and western Victoria.

Sclerocyphon lacustris sp.n.

(Figures 3.52-3.56, Pls 3.25-3.27)

Material Examined

Types - TASMANIA (all Interlaken Point, Lake Sorell, coll. J.A. Smith): holotype ♀, in spirit with pupal and larval exuviae, (TM Reg. No. F1331), 6.*xii*.1978; allotype ♂, in spirit with pupal and larval exuviae, (TM Reg. No. F1332), 28.*xii*.1978. Paratypes: 1 ♀, 13.*xii*.1978, 1 ♂, 24.*xi*.1978, 5 L, 2.*x*.1979, ANIC; 1 ♀ (TM Reg. No. F1333) 6.*xii*.1978, 1 ♂ (TM Reg. No. 1334), 6.*xii*.1978, 5 L (TM Reg. No. 1335), 2.*x*.1979, TM; 1 ♀, 1 ♂, in spirit with genitalia dissected, in smaller vial, 1 ♀, 1 ♂, dried, 6.*xii*.1978, 5 L, 2.*x*.1979, NMV.

Other material examined - TASMANIA: 28 ♀♀, 22 ♂♂, plus pupal and larval exuviae, Interlaken Point, Lake Sorell, larvae coll. Oct. 1978, J.A. Smith, emerged in lab. Nov. and Dec. 1978; 3 ♀♀, 2 ♂♂, Interlaken Point, Lake Sorell, 30.*xii*.1978, J.A. Smith; 2 ♀♀, 1 ♂, Interlaken Point, Lake Sorell, 29.*xii*.1978, A.M.M. Richardson; 1 L, Lake Sorell, 12.*v*.1975, B. Knott; 13 L, Lake Sorell, 6.*iii*.1975, J.A. Smith; 14 L, Canal between Lake Sorell and Lake Crescent, 6.*iii*.1975, J.A. Smith; 1 L, Lake Crescent, 1973, P. Roberts; 3 L, Lake Pillans, 16.*ii*. 1963, W. Mollison; 4 L, Lake Field (Central Plateau), 25.*ii*.1978, W. Fulton; 1 L, Little Blue Lake, nr Lake Augusta, 20.*ix*.1978, V. Dell; 2 ♀♀, 13 L, Ada Lagoon, 22.*i*.1979, W. Fulton; 10 L, Lake Ada, 22.*i*.1979, W. Fulton; 6 L, Lake Baillie, 22.*i*.1979, W. Fulton; 1 ♀, 5 L, Talinah Lagoon, 20.*i*.1979, W. Fulton; 4 L, Interlaken, Lake Sorell, Feb.1963, WDW; 5 L, Pine Lake, Feb.1963, WDW; 3 L, Dove Lake, nr Cradle Mt., Feb.1963, WDW; 1 L, Clarence Lagoon, Feb.1963, WDW; 1 L, Lake Augusta, Feb.1963, WDW; 4 L, small unnamed lagoon between Lake Ada and Lake Augusta, Feb.1963, WDW; 1 L, Dove Lake, Cradle Mountain-Lake St. Clair

National Park, 10.*ii*.1967, E.F. Riek, ANIC; 2 L, Dove Lake, 18.*x*.1972, PZ; 1 L, Shadow Lake, nr Lake St. Clair, 10.*x*.1972, PZ; 10 L, Lake Sorell, 16.*x*.1972, PZ; 3 L, Lake Crescent, 15.*x*.1972, PZ; 2 L, Great Lake, northern end, from ditch of still water, Jan.1953, CW.

Description

Female (Figures 3.52-3.54)

Total length 6.0 mm, head width 1.1 mm, pronotal length 1.25 mm, pronotal width 3.0 mm, width between apical angles of pronotum 1.3 mm, scutellar length 0.4 mm, scutellar width 0.5 mm, elytral length 4.6 mm, elytral width 3.6 mm.

General shape - Elongate-elliptic subconvex beetle.

Head - Dark brown/black.

Pronotum - Uniformly dark brown overall, covering of fine ashen pubescence, dense laterally, sparser medially where moderately shiny, punctate derm visible. Small irregular clumps of coarse white pubescence across middle. Medial region convex, lateral margins wide, flat, yellow.

Elytra - Uniformly dark brown, almost black, covering of fine ashen pubescence overall, densest laterally and apically. Apical third with small clumps of dense, coarse white pubescence. Medial region of basal third with some glabrous patches, derm moderately shining, transverse wrinkles extending from suture. Elytra widest at apical third, gently convex, medial region flattened. Large, very shallow, transverse marginal impression on lateral margin, in basal third, on each side. Lateral margins narrow, yellow.

Legs - Femur black, tibia black, tarsi brown.

Thorax - Pro- and mesosternum yellow, metasternum black, antecoxal piece yellow.

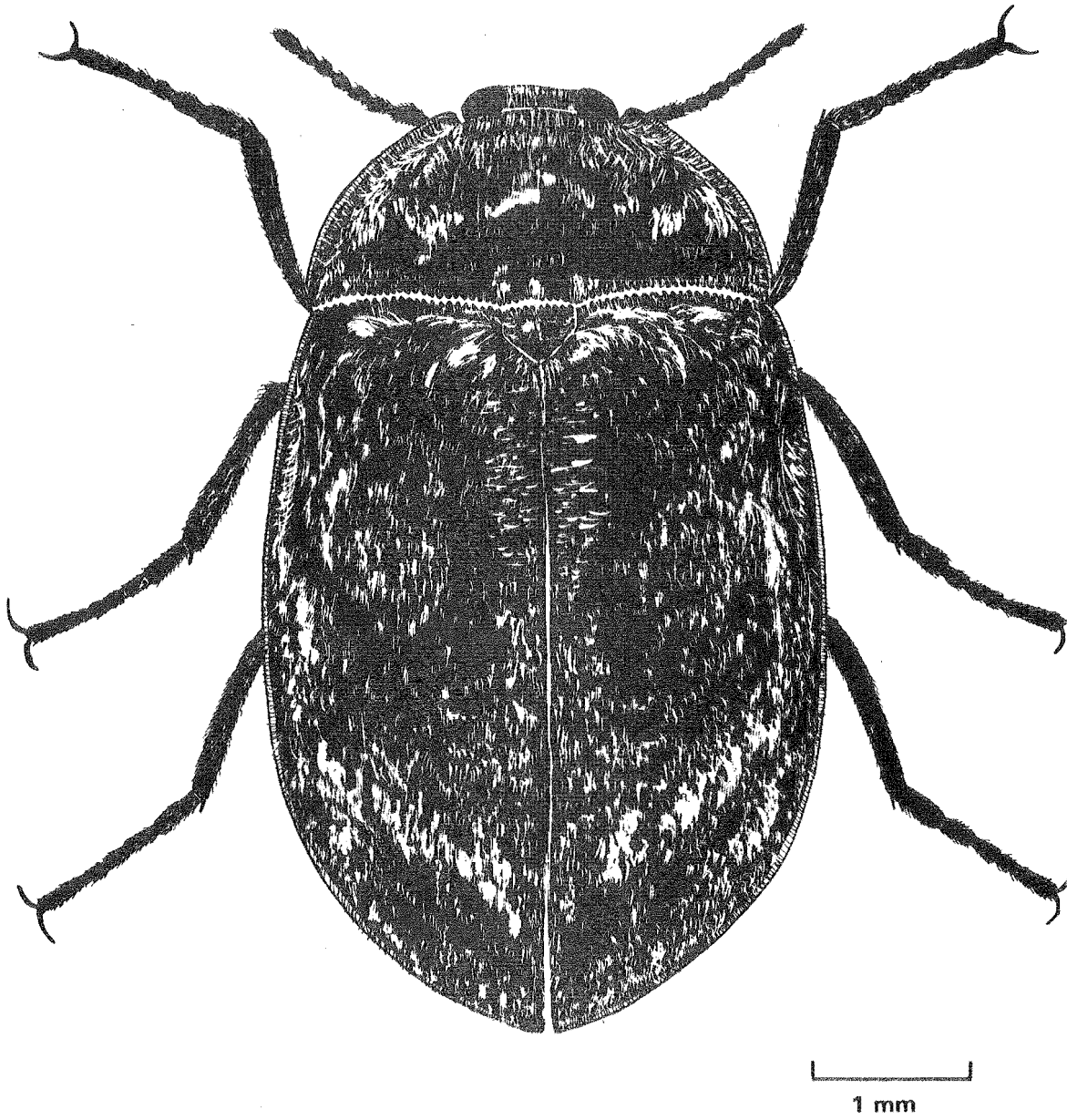


FIGURE 3.52 *Sclerocyphon lacustris*, ♀, holotype, dorsal view. Scale line = 1 mm.

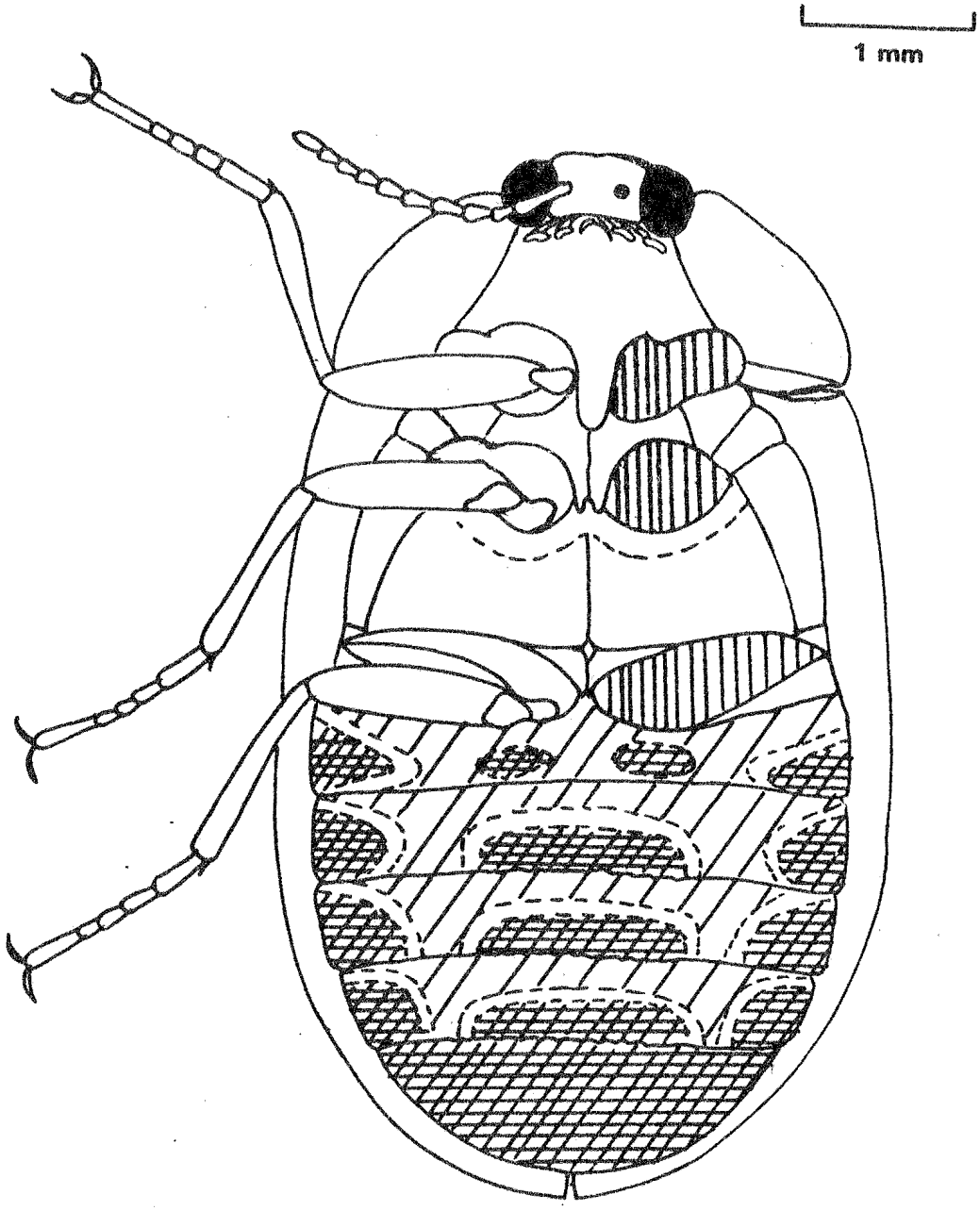
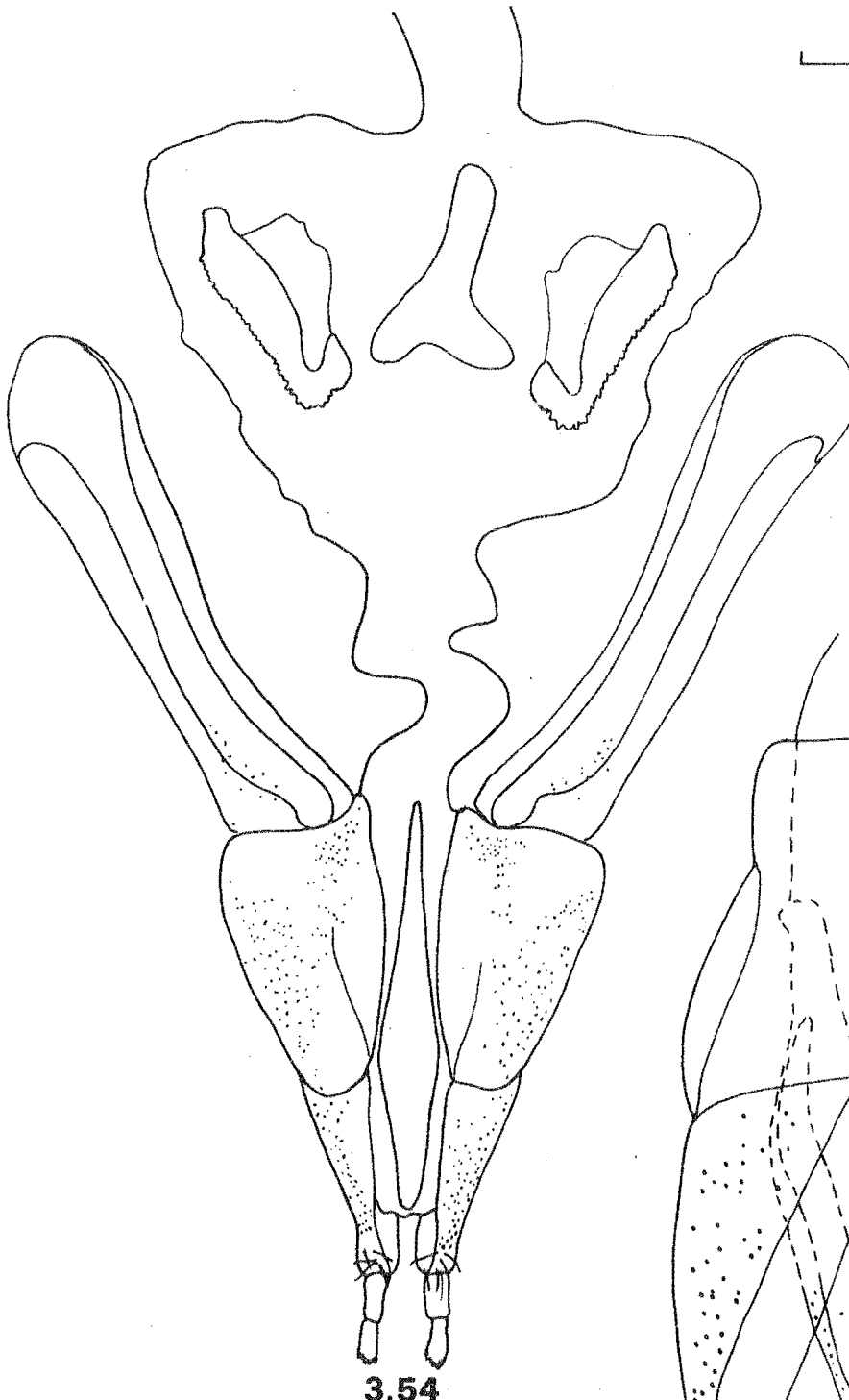
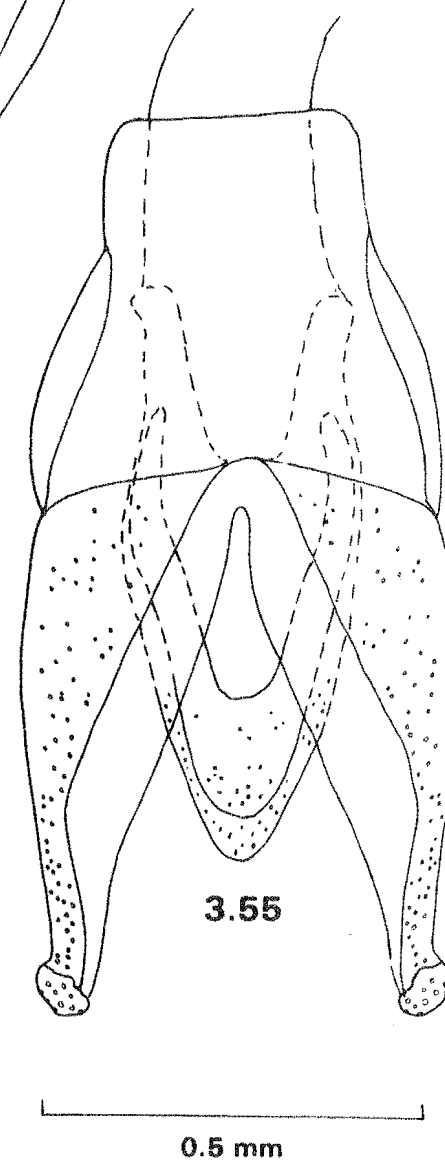


FIGURE 3.53 *Sclerocyphon lacustris*, ♀, holotype, dorsal view. Scale line = 1 mm.





FIGURES 3.54-3.55 *Sclerocyphon lacustris*, ♀ external genitalia, ventral view; (3.55) ♂ external genitalia, ventral view. Scale lines = 0.5 mm.

Abdomen (Figure 3.53) - Segments 1-4 black medially and laterally, narrowly outlined with yellow, remainder light brown. Segment 5 black overall.

External genitalia (Figure 3.54) - Pair of sclerotised hemisternites punctate, setose distally, bearing 2-segmented styli. Sclerotised rod, embedded in vaginal wall between hemisternites, expanded at middle, narrow anteriorly and posteriorly. Pair of sclerotised plates, embedded in anterior dorso-lateral vaginal walls, relatively long, expanded anteriorly.

Male (Figure 3.55)

Total length 4.7 mm, head width 0.1 mm, pronotal length 1.0 mm, pronotal width 2.6 mm, width of pronotum between apical angles 1.15 mm, scutellar length 0.35 mm, scutellar width 0.45 mm, elytral length 3.6 mm, elytral width 2.9 mm.

Similar to female but smaller, lighter brown, sparser and more irregular covering of ashen pubescence.

External genitalia (Figure 3.55) - Aedeagus symmetrical, trilobate. Parameres sclerotised, punctate, relatively short, narrowing to membranous tips. Penis complex, consisting of two sclerites, dorsal sclerite wide anteriorly, lateral margins tapering to rounded apex. Ventral sclerite narrower but nearly as long as dorsal sclerite.

Last instar larva (Figure 3.56, Pls 3.25-3.27)

Total length 9.5 mm, total width 5.5 mm, length of ninth tergite 1.6 mm, width of ninth tergite 1.9 mm.

General shape - Elongate-elliptic thoraco-abdominal shield, widest at metanotum/tergite 1, tapering to tergite 9.

Dorsal surface - Medial region dark brown/black, yellow patches on tergites 1, 2, 3 and 5, 6, 7, tergites 4, 8 and 9 completely dark.

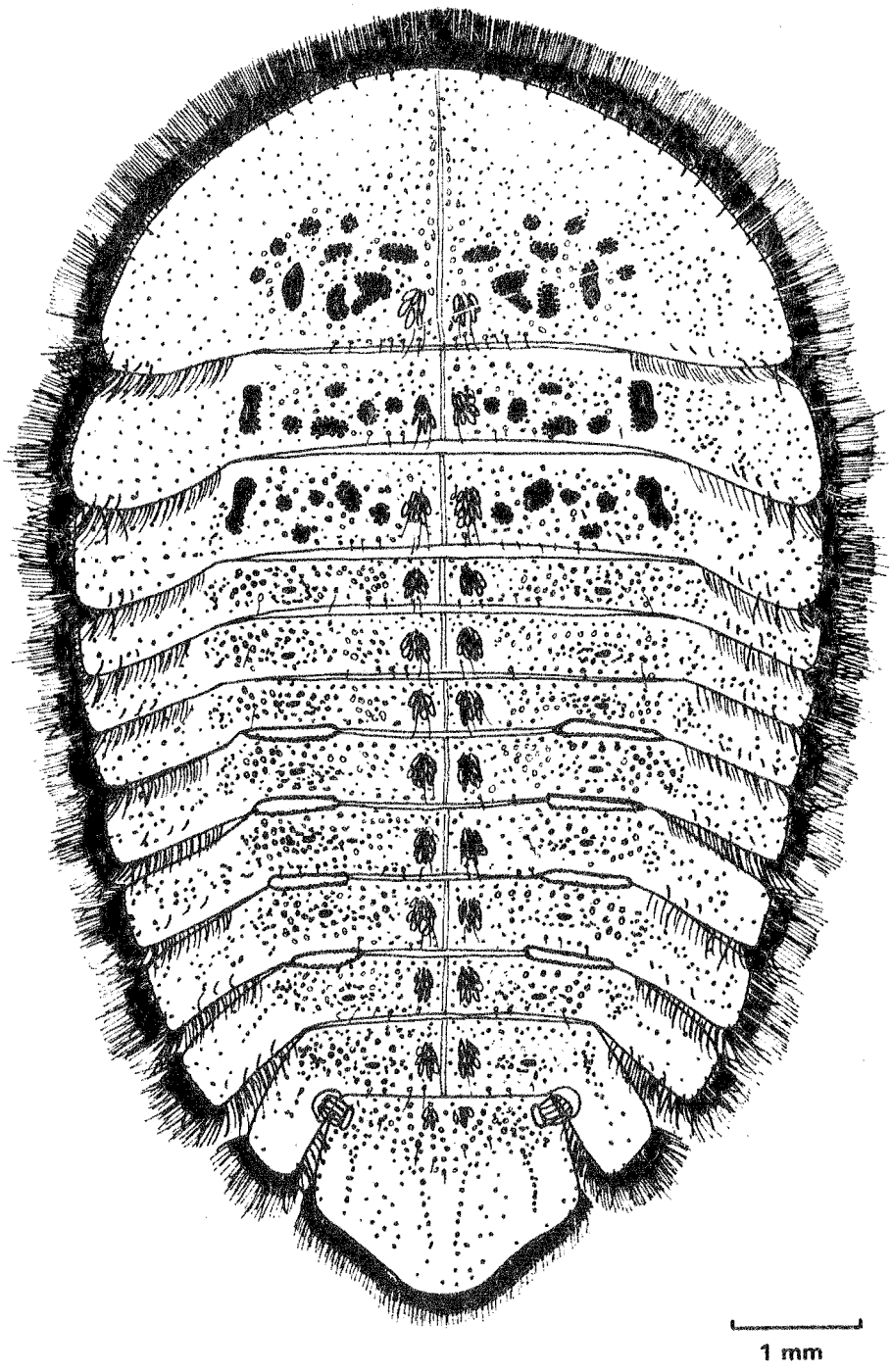
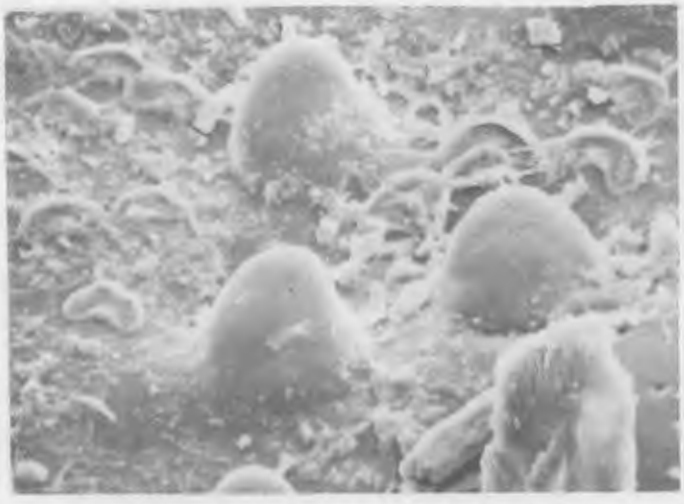


FIGURE 3.56 *Sclerocyphon lacustris*, last instar larva, paratype, dorsal view. Scale line = 1 mm.

3.25

3.26



3.27

PLATES 3.25-3.27 *Sclerocyphon lacustris*, last instar larva from Lake Sorell, tergite 9: (3.25) x 40; (3.26) x 200; (3.27) x 650.

Lateral laminae light brown with yellow patch near margin.

Entire marginal fringe of setae with 2 bands visible, narrow, yellow inner section, wide transparent outer section. Overlying this a sparser irregular fringe of dark brown, randomly orientated setae, slightly longer than regular fringe. Trailing edge of lateral laminae with fringe of fine transparent setae plus some longer dark brown, randomly orientated setae, denser towards lateral margins.

Fairly uniform covering of large, dark, pointed, cuticular beads. Dark denser clumps of beads at junction of lateral laminae and body on tergites 1-8. Medial region with beads smaller than those on lateral laminae, beads sparser towards ends of laminae.

Pores scattered over entire surface, densest regions, beneath coat of shining, grey mucus, between pits on pro-, meso- and metanotum and extending across tergites 1-8 with two main regions, each side of ecdysial scar, each side of midline. Some pores with fine hairs.

Twelve paired groups of trichoid sensilla in medial region, one group to each side of midline on each thoracic and abdominal segment. Discrete, shining, grey, mucus-coated sensilla visible, in elongate-oval clumps, each pair widely separated across midline. Some clumps with long, shining, backward-trailing hairs.

Pronotum with 5 pairs of irregular pits and 4 pairs of circular pits. Meso- and metanotum with 6 pairs of irregular pits. Most pits dark, some pale, all bordered by beads.

Four pairs of gin traps present on adjoining margins of tergites 3-4, 4-5, 5-6, 6-7. Three anterior pairs wide, posterior pair narrow. Upper margin of each gin trap finely sclerotised, lower margin darker, heavily sclerotised.

Tergite 9 (Pls 3.25-3.27) with faintly upraised central ridge extending only to middle of tergite, not the apex, plus a lesser ridge on each side, all outlined by beads. Posterior region flattened,

beads sparse. Posterior margin produced medially in deep regular semi-circle bordered each side by a concave sinuosity, apical angles curved. Lateral margins sloping, slightly curved.

Diagnosis

Adults can be distinguished by the following combination of characters; elongate-elliptic body, dense covering of fine pubescence, uniform colour, moderately shining derm, relatively wide penile sclerites or long anteriorly expanded vaginal plates.

Larvae can be distinguished by the following combination of characters; 4 gin traps, tergite 9 with its weakly upraised short ridges outlined with cuticular beads and posterior margin produced in a deep, regular semi-circle, cuticular beads with pointed apices (best seen by scanning electron microscopy), discrete mucus-coated sensilla arranged mid-dorsally in elongate clumps, and the many fine hairs extending from pores over the entire dorsal surface.

Comments

S. lacustris is endemic to Tasmania and it appears to be restricted to the wave-swept rocky shores of the lakes of the Central Plateau. The specific epithet has been chosen to emphasize the lake-dwelling existence of the species.

Large numbers of larvae are present in Lake Sorell, one of the few lakes of the Central Plateau unaltered by hydro-electric development. Last instar larvae leave the water to pupate under logs and rocks at the lake's edge. Approximately 150 pupae were counted beneath one log on the bank although the numbers of larvae in the lake adjacent to this region had always been considerably lower. As Lake Sorell is a large, shallow lake larval distribution probably extends over most of it, wherever a suitable rocky substrate is present, with larvae only congregating

in large numbers at suitable, but more restricted, pupation sites on the shore.

Adults and larvae were linked both by the rearing of adults from larvae held in the laboratory and field collection of newly emerged adults still associated with their larval and pupal exuviae.

A heavier coating of mucus and profusion of extra setae on the dorsal shield were observed more often on the larvae of this lake-dwelling species than on most stream-dwelling species and therefore may be regarded as a response to some environmental factor (or factors) more prevalent under lake conditions than stream conditions. Temperature fluctuations within the shallow Plateau lakes are probably much greater than those experienced in most Tasmanian streams. Wave action on the lakes is dependent upon prevailing wind conditions and still water conditions may exist for considerable periods of time. The increased production of setae and mucus may be a response to fluctuations in temperature or periodical still conditions.

Sclerocyphon minimus sp.n

(Figures 3.57 - 3.61)

Material Examined

Types - QUEENSLAND: (all Crystal Cascades via Cairns, G. Monteith, QU) holotype ♀, QM Reg. No. 8467, 30.*xii*.1963, QM; allotype ♂, 22.*ii*.1964, QU. Paratypes: 1♂, 1♂ (with genitalia dissected, in vial), 6♀♀, 7♂♂, 30.*xii*.1963, QU; 7♀♀, 6♂♂, 22.*xii*.1965, QU; 1♀, 6.*xii*.1966, B. Cantrell, QU; 1♀, 1♂, 30.*xii*.1963, ANIC; 2♀♀, 2♂♂, 30.*xii*.1963, NMV.

Other material examined - QUEENSLAND: 1♀, 11♂♂ (29.*xii*.1964), 3♀♀ (5.*xii*.1965), all Henrietta Ck., Palmerston Nat. Park, G. Monteith, QU; 4♀♀, Mossman Gorge via Mossman, 25-26.*xii*.1964, G. Monteith, QU; 1♀, 1♂, Gap Ck., 6 mi. N of Bloomfield R., 13.*xi*.1965, G. Monteith, QU; 3♀♀, 2♂♂, Gap Ck., 5 mi. N of Bloomfield R., 13.*xi*.1965, G. Monteith, QU; 2♀♀, 2♂♂, Upper Daintree R. via Daintree; 27.*xii*.1964, G. Monteith, QU; 1♀, 1♂ (15.*xii*.1966), 4♂♂ (15.*xi*.1969), all "The Boulders" via Babinda, B. Cantrell, QU; 1♀ (9.*i*.1964), 1♀ (4.*xii*.1965) all Millaa Millaa Falls, G. Monteith, QU; 1♂, McIvor R., 40 mi. N of Cooktown, 7.*v*.1970, G. Monteith, QU; 1♂, Millers Crossing, 30 mi. N of Cooktown, 24-25.*xi*.1965, G. Monteith, QU; 1♀, Laceys Ck., Mission Beach, 21.*iv*.1970, G. Monteith, QU; 1♀, Upper Mulgrave R., 1-3.*xii*.1965, G. Monteith, QU; 1♀, Paluma Dam, 27.*xii*.1963, G. Monteith, QU; 1♀, 1♂, Mt. Mee via Dayboro, 12.*iii*.1967, K.J. Chandler, QU; 7♀♀, 6♂♂ (23.*i*.1965), 2♀♀ (29.*i*.1965), 1♂ (5-6.*xii*.1965), 2♀♀, 3♂♂ (Jan. 1965), 1♀ (17-23.*i*.1966), 5♀♀, 3♂♂ (Feb. 1966), 1♀ (14.*xii*.1966), 1♂ (16.*xi*.1966), 2♂♂ (26.*xi*.1966), 1♂ (10.*xii*.1966), 4♂♂ (31.*iii*.1967), 6♂♂ (2.*iv*.1967) all Cardstone, J.G. and J.A.G. Brooks, ANIC; 2♀♀, 4♂♂ (*ii*.1966), 1♀ (1.*ii*.1966), 1♀, 1♂ (2.*ii*.1966), 1♀ (17-23.*ii*.1966) all Cardstone, K. Hyde, ANIC; 3♀♀ (Dec. 1964), 1♀ (28.*xii*.1964) all Archers Ck., J.G. Brooks, ANIC; 3♂♂, Koomboologoba, Dec. 1964, J.G. Brooks, ANIC; 2♀♀, 2♂♂, Station Ck., Jan. 1964, J.G. Brooks, ANIC; 2♀♀, 2♂♂, Mossman

Gorge rainforest, at light, 28.*x*.1966, E.B. Britton, ANIC; 1♀, Boar Pocket Rd., 8 km N of Gillies Hwy, at light, 21.*ii*.1970, J.G. Brooks, ANIC.

NEW SOUTH WALES: 1♀, Minnamurra Falls, 10 mi. N Kiama, 23.*xii*.1974, H. and A. Howden, ANIC; 5♀♀, 6♂♂, Minnamurra Falls, via Kiama, 9.*i*.1967, G. Monteith, QU; 5♀♀, 7♂♂, Barrington House, via Salisbury, 7.*i*.1967, G. Monteith, QU; 1♀, Gloucester, 11.*v*.1946, H.J. Carter, ANIC; 1♀, Williams R., Dungog, *xi*.1926, H.J. Carter, ANIC; 1♀, Williams R., *x*.1926, H.J. Carter, ANIC.

Description

Female (Figures 3.57 - 3.58, 3.60)

Total length 3.8 mm, head width 0.8 mm, pronotal length 0.7 mm, pronotal width 2.15 mm, width between apical angles of pronotum 0.95 mm, scutellar length 0.3 mm, scutellar width 0.35 mm, elytral length 3.05 mm, elytral width 2.65 mm.

General shape - Small, oval, convex beetles.

Head - Light brown.

Pronotum - Light brown with some yellow patches, fine dense pubescence laterally, relatively glabrous, derm shining medially, some glabrous patches along base. Medial region gently convex, sloping to lateral margins. Lateral margins narrow, yellow. Apical angles sharp.

Scutellum - Light brown outlined with yellow, nearly as broad as long.

Elytra - Dark brown apically and laterally, medial region adjoining scutellum and elytral suture (to middle) yellow, relatively glabrous, derm shining, punctures and fine transverse wrinkles visible. Apical third with dark brown glabrous crescent, on each side of suture, bordered anteriorly and posteriorly by coarse white pubescence. Fine ashen pubescence plus clumps of coarse white pubescence apically and laterally.

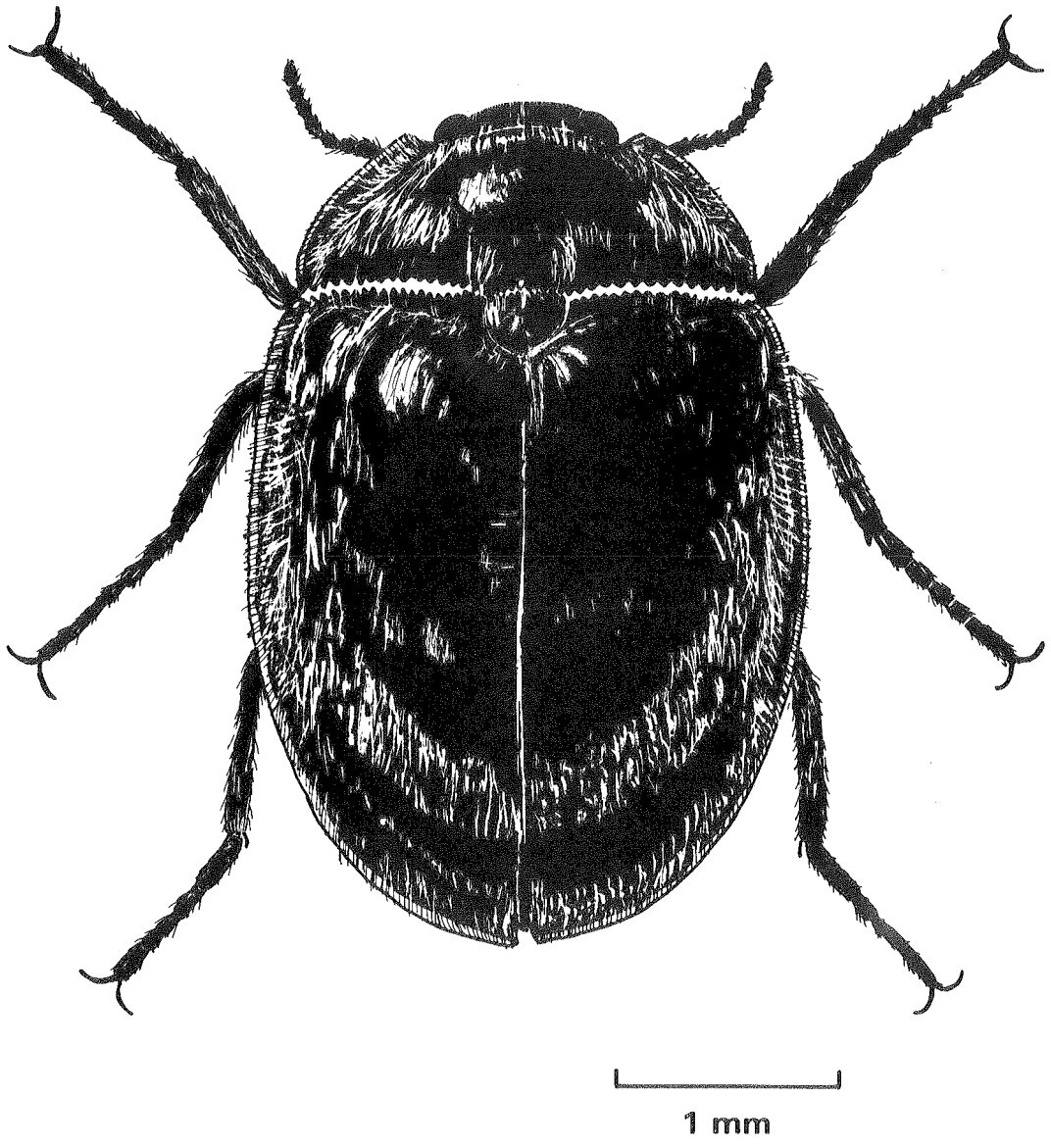
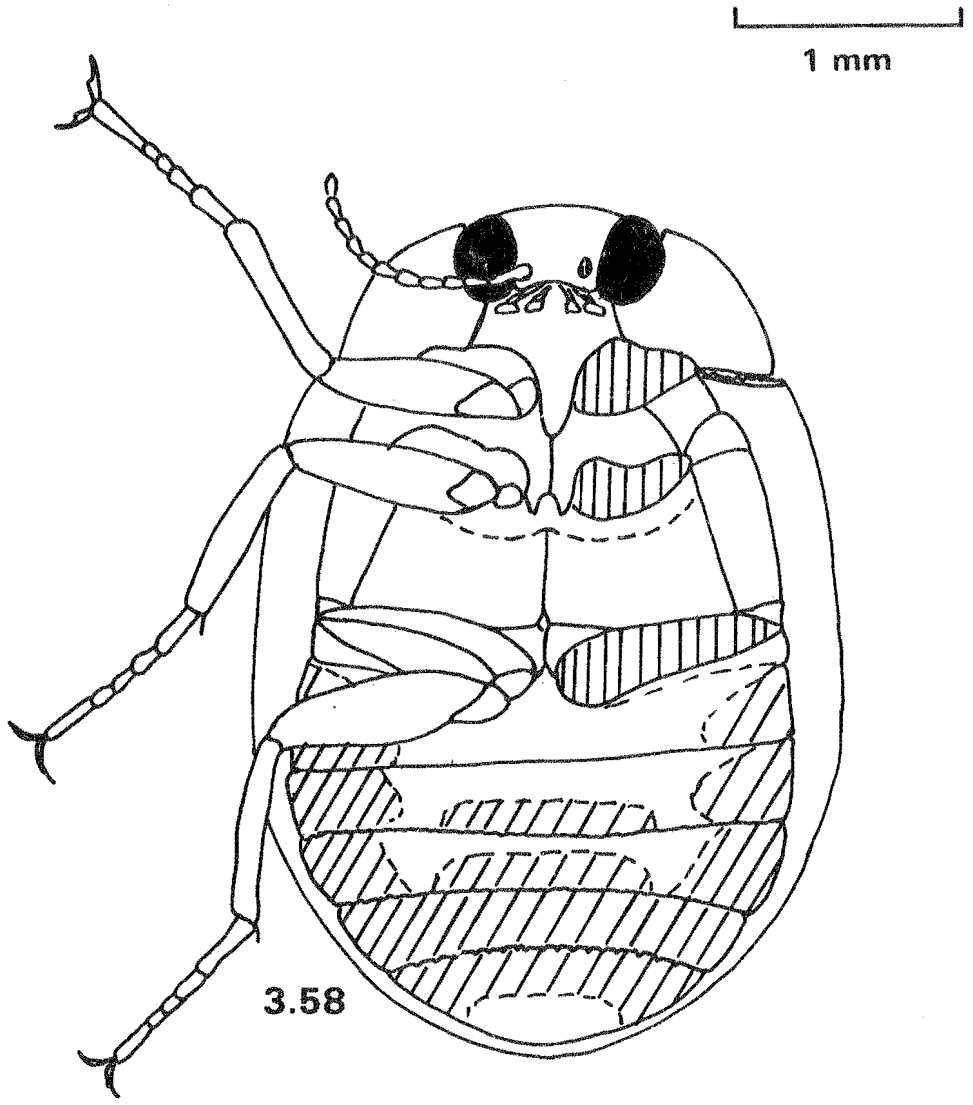
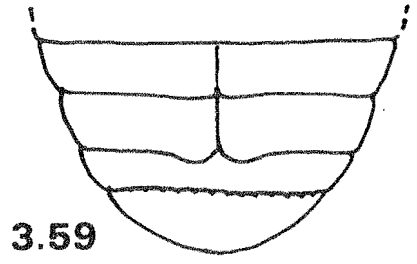
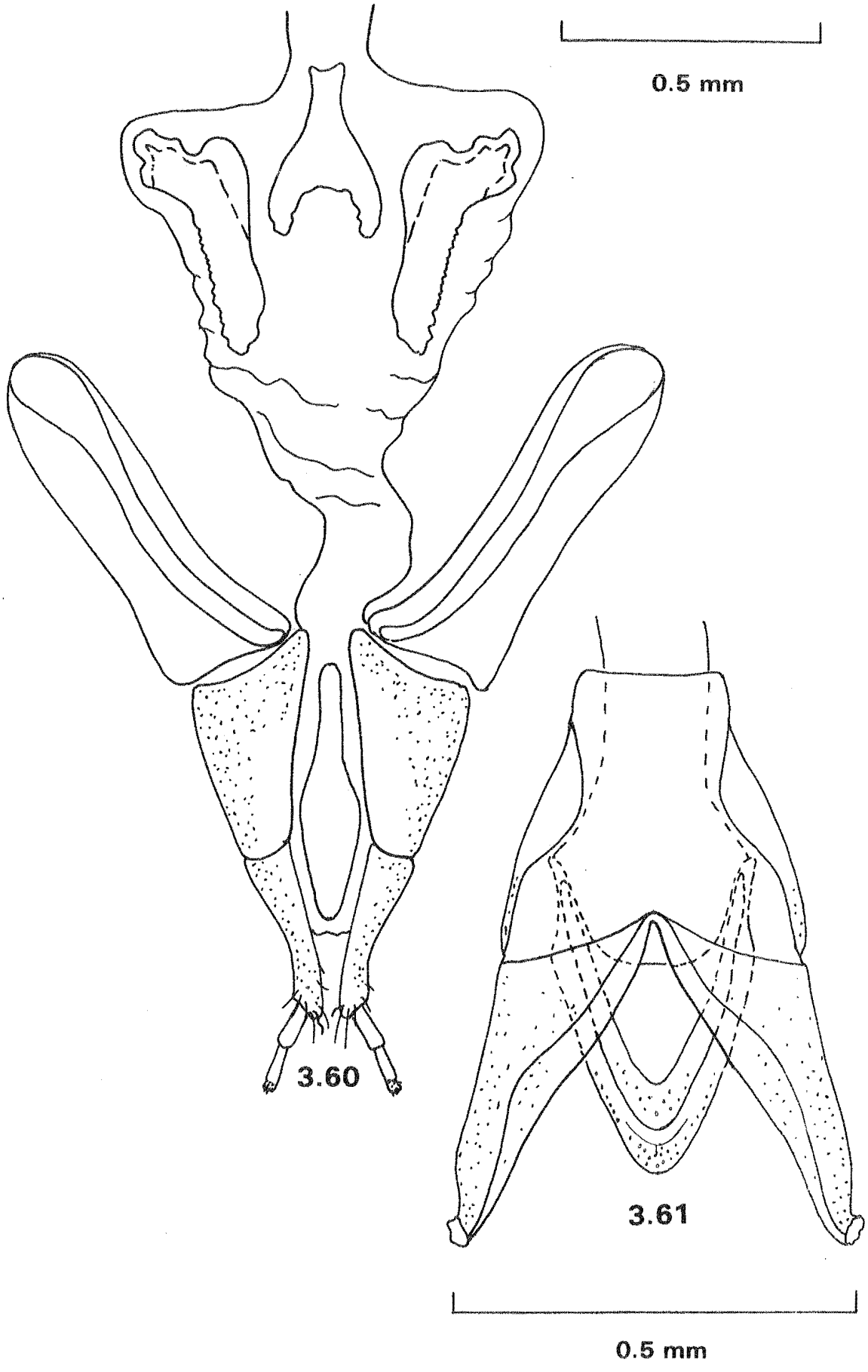


FIGURE 3.57 *Sclerocyphon minimus*, ♀, holotype, dorsal view. Scale line = 1 mm.





FIGURES 3.58-3.59 *Sclerocyphon minimus:* (3.58) ♀, holotype, ventral view; (3.59) ♂, abdomen, ventral view. Scale line = 1 mm.



FIGURES 3.60-3.61 *Sclerocyphon minimus*: (3.60) ♀, external genitalia, ventral view; (3.61) ♂, external genitalia, ventral view. Scale lines = 0.5 mm.

Striations faintly visible in lateral regions. Elytra convex, gently sloping from suture to lateral margins, sharply sloping in apical region, widest just past midpoint then curving quickly around to apex. Shallow transverse marginal impression, on each side, below glabrous shoulder. Lateral margins narrow, yellow.

Legs - Femur dark brown, tibia and tarsi yellow.

Thorax - Pro-, meso- and metanotum and antecoxal piece yellow.

Abdomen (Figure 3.58) - Predominantly brown, yellow medially.

External genitalia (Paratype) (Figure 3.60) - Pair of sclerotised hemisternites, punctate, setose distally, bearing 2 segmented styli. Sclerotised rod embedded in vaginal wall between hemisternites, broad expanded at middle. Pair of sclerotised plates, embedded in anterior dorso-lateral vaginal walls, with strongly sclerotised convoluted anterior margin tapering to long, narrow apex.

Male (Figures 3.59, 3.61)

Total length 3.2 mm, head width 0.75 mm, pronotal length 0.7 mm, pronotal width 1.75 mm, width between apical angles of pronotum 0.8 mm, scutellar length 0.25 mm, scutellar width 0.25 mm, elytral length 2.45 mm, elytral width 2.2 mm.

Pronotum - Covered entirely with ashen pubescence.

Elytra - Dense, ashen pubescence overall except for two pairs of glabrous, dark brown patches, either side of medial line, anterior pair extending in crescent from suture, just past midline, posterior pair extending in narrow strip from suture, near apex.

Abdomen (Figure 3.59) - Segment 3 upraised and strongly produced posteriorly either side of midline, thick pubescence parted along midline, sweeping to either side. Segment 2 with similar midline part in pubescence but only weakly produced posteriorly.

External genitalia (Paratype, Figure 3.61) - Aedeagus symmetrical,

trilobate. Parameres sclerotised, punctate, narrowing to membranous tip. Penis complex, consisting of two sclerites, dorsal sclerite wide, lateral margins tapering to rounded apex, ventral sclerite similar, but shorter, narrower.

Diagnosis

Adults can be distinguished by the following combination of characters; oval, convex body and brown/light brown dorsal surface with fine pubescence and one or two glabrous crescents either side of suture at midline and apex of elytra. Males are easily recognised by the midline parting in pubescence and the posterior prolongation of abdominal segment 3, also present, but to a lesser extent, on segment 2. The two vaginal plates with strongly sclerotised and convoluted anterior margins and long narrow apices are also diagnostic.

Comments

The specific epithet was chosen in recognition of the fact that many members of this species represent the smallest beetles of *Sclerocyphon* found so far, some males being only 3 millimetres in total length.

No larval form has been linked with this adult yet, however it is probable that one of the larval types described below may be the larva of this species. In particular, *S* type C exhibits a similar pattern of distribution; however, laboratory rearing of adults from larvae is needed for a positive adult-larva assocation.

The distribution of this species ranges from the McIvor River, 40 miles north of Cooktown, in north Queensland, to Minnamurra Falls near Kiama on the south coast of New South Wales. However, this species appears to be a predominantly northern one as the greatest number of beetles have been recorded from the Cairns-Atherton district of north Queensland.

Sclerocyphon nitidus sp. n.

(Figures 3.62 - 3.65)

Material Examined

Types - QUEENSLAND: holotype ♀, Lamington National Park, QM Reg. No. 8468, 21.*xi*.1965, B. Cantrell, QM; allotype ♂ (genitalia dissected, in vial), National Park, Jan. 1928, H.J. Carter, ANIC. Paratypes: (all Lamington National Park, 21.*xi*.1965), 1♀, B. Cantrell (QU) ANIC; 1♀, T. Weir (QU) NMV; 3♀♀ (genitalia of one dissected, in vial) T. Weir, QU.

Other material examined - QUEENSLAND: 4♀♀, Durimbah, Jan. 1964, Coll?, SAM; 1♀, National Park, Macpherson Range, Jan. 1928, H.J. Carter, ANIC. NEW SOUTH WALES: 1♀, National Park, date?, Lea, SAM; 1♀ Whian Whian State Forest, via Dunoon, 700' 25-56.*xi*.1972, G. Monteith. QU.

Description

Female (Figures 3.62-3.65)

Total length 6.3 mm, head width 1.2 mm, pronotal length 1.2 mm, pronotal width 3.5 mm, width between apical angles of pronotum 1.5 mm, scutellar length 0.4 mm, scutellar width 0.5 mm, elytral length 5.0 mm, elytral width 4.65 mm.

General shape - Relatively large, very convex, oval to circular beetles.

Head - Red-brown.

Pronotum - Medial region red-brown with irregular black patches, lateral regions red-yellow. Medial region relatively glabrous, shining, punctate, convex with medial line faintly visible. Lateral regions with fine, dense, ashen pubescence, flattened. Apical angles blunt.

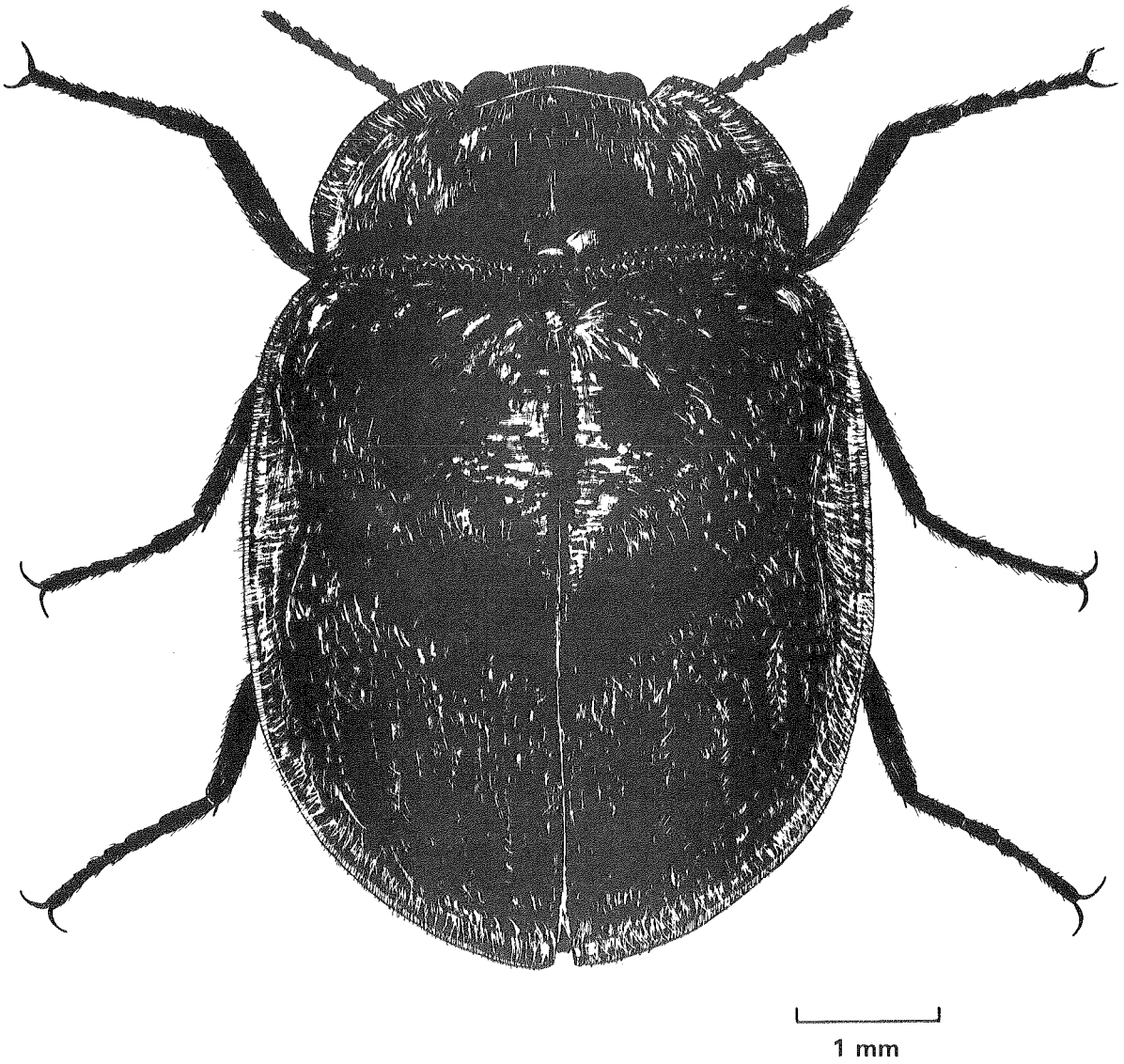


FIGURE 3.62 *Sclerocyphon nitidus*, ♀, holotype, dorsal view. Scale line = 1 mm.

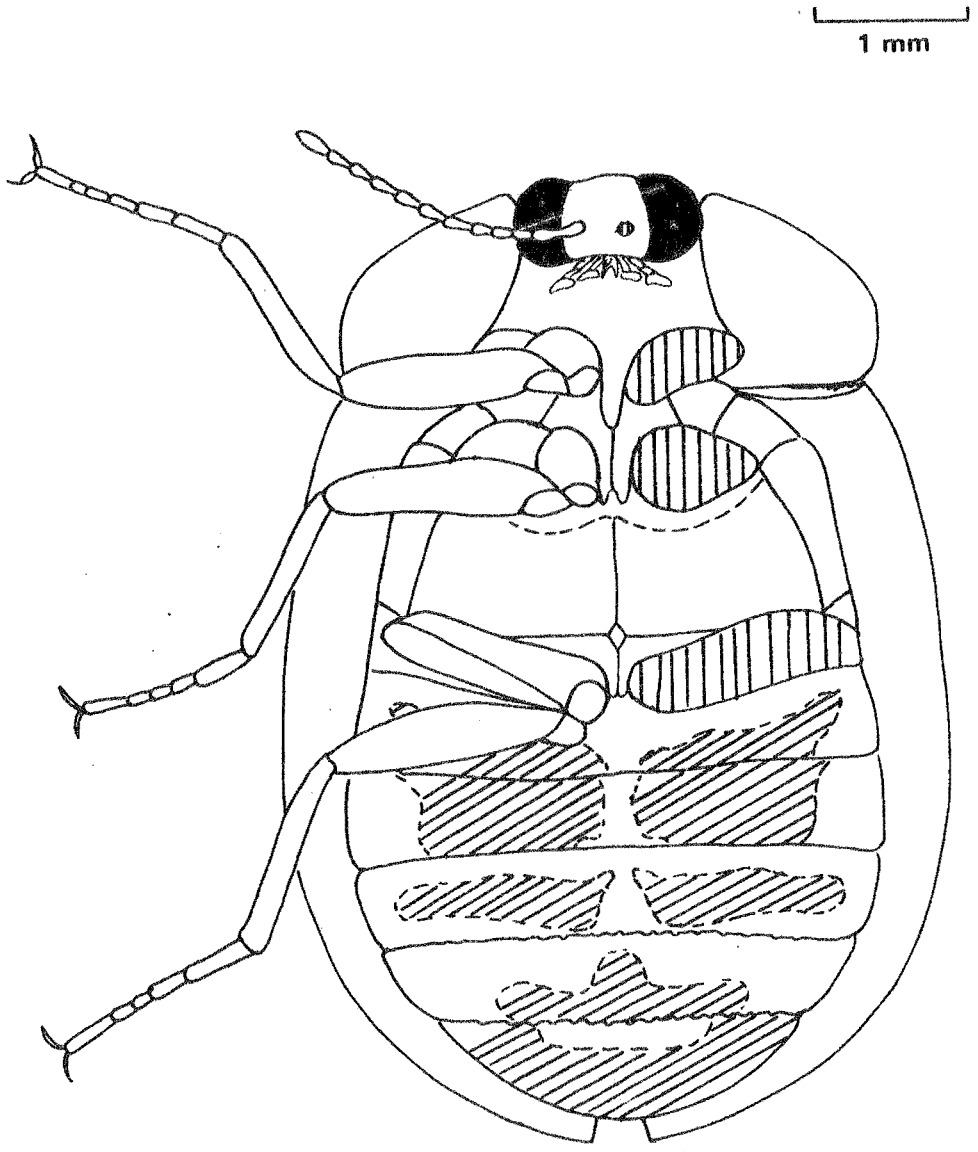
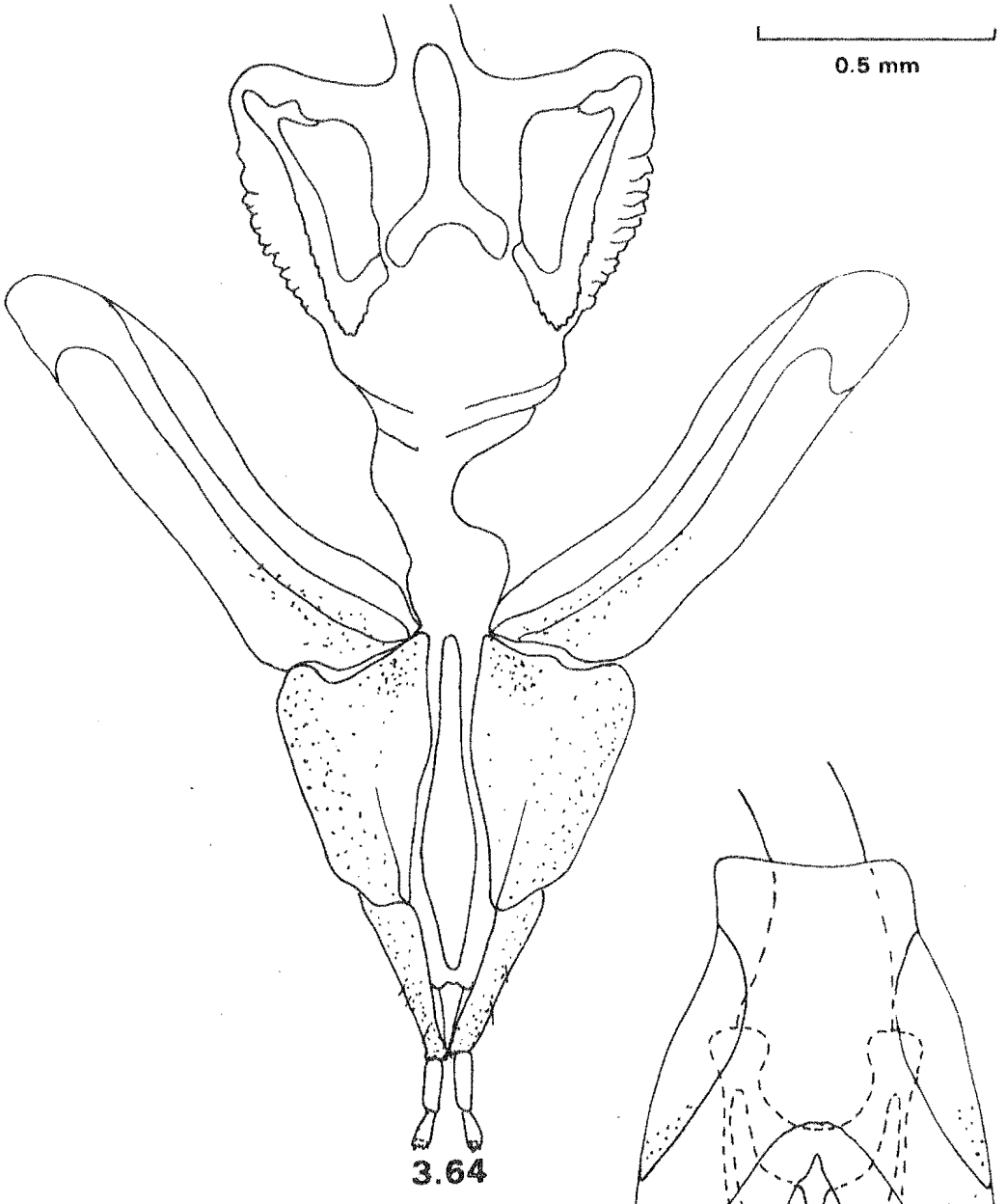
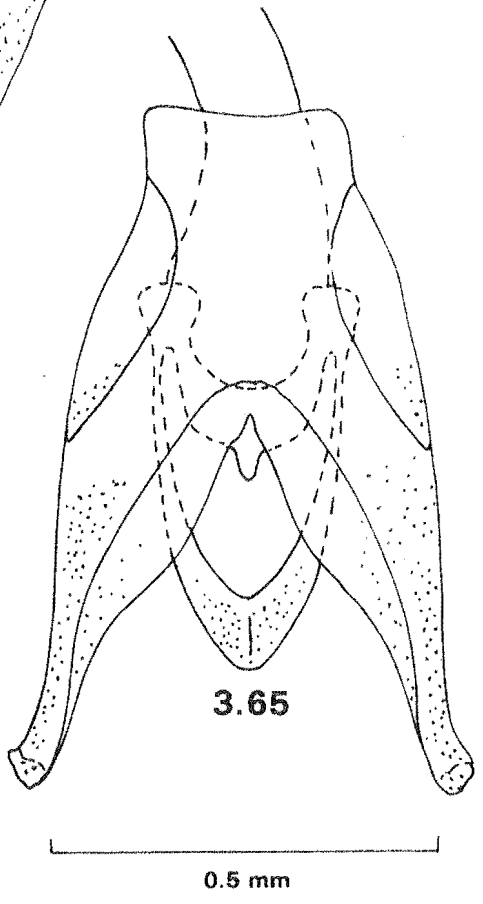


FIGURE 3.63 *Sclerocyphon nitidus*, ♀, holotype, ventral view. Scale line = 1 mm.





FIGURES 3.64-3.65 *Sclerocyphon nitidus:* (3.64) ♀, external genitalia, ventral view; (3.65) ♂, external genitalia, ventral view. Scale lines = 0.5 mm.

Scutellum - Red.

Elytra - Red-yellow, with some small dark patches, in medial basal region and either side of suture to middle, black laterally and apically. Medial basal region glabrous, shining, punctate, transverse wrinkles extending from suture visible. Small clumps of coarse white pubescence scattered over entire surface, densest laterally and above and below dark, glabrous patch in middle third. Very deep, wide transverse marginal impression below shoulder on each side. Elytra very convex, broad and raised in comparison to pronotum, highest and widest at middle. Striations visible laterally and apically, outlined by longitudinal rows of pubescence. Margins very wide, flat, yellow.

Thorax - Pro- and mesosternum yellow, metasternum black with ante-coxal piece yellow.

Legs - Femur black, tibia brown, tarsi yellow.

Abdomen - (Figure 3.63). All segments predominantly light, red-yellow, with black patches medially.

External genitalia (Paratype, Figure 3.64) - Pair of sclerotised hemisternites, wide proximally, narrow and setose distally, punctate, bearing 2-segmented styli. Sclerotised rod, embedded in vaginal wall between hemisternites, expanded at middle. Sclerotised plates embedded in anterior dorso-lateral vaginal walls, long and narrow, anterior and posterior apices pointed.

Male (Figure 3.65)

Total length 4.4 mm, head width 0.95 mm, pronotal length 0.95 mm, pronotal width 2.45 mm, width between apical angles of pronotum 1.2 mm, scutellar length 0.3 mm, scutellar width 0.4 mm, elytral length 3.35 mm, elytral width 3.1 mm.

Similar to female but smaller.

Abdomen - Segment 3 with pubescence parted at midline.

External genitalia (Allotype, Figure 3.65) - Aedeagus symmetrical, trilobate. Parameres narrow, sclerotised, punctate, with membranous tips. Penis complex, consisting of two sclerites, dorsal sclerite short with lateral margins tapering to narrow apex, ventral sclerite similar but not as long, also narrower.

Diagnosis

Adults can be distinguished by the following combination of characters; shining dorsal surface, elytra broad in comparison to pronotum, swollen with greatest height and width at middle and wide flattened margins, and the form of the penile sclerites or vaginal plates (illustrated in Figures 3.65 and 3.64, respectively).

Comments

Although only a limited number of specimens were examined (13♀♀ and 1♂) their distinctive morphology warranted their description as a new species. The specific epithet, meaning "shining" was chosen because of the extremely shiny dorsal surface exhibited by all specimens.

As yet no adult-larva association has been obtained. It is possible that *S* type D (described below) is the larval form of this species, by virtue of its similar distribution, (it has been recorded only in Lamington National Park).

Sclerocyphon zwicki sp.n.

(Figures 3.66 - 3.70, Pls 3.28 - 3.30)

Material Examined

Types - VICTORIA: holotype ♀, Macalister-Barkly R.jn, Lyndon Flat, MV light, 6.*xii*.1977, NMV-SD; allotype ♂, same data as holotype, ANIC. Paratypes: 4♀♀, 1♂, same data as holotype, NMV; 5 L, Macalister-Barkly R.jn, Lyndon Flat, 24.*ii*.1978, NMV-SD, NMV.

Other material examined - VICTORIA:- 2♀♀, 6♂♂, Thomson R., Bells Clearing, MV light, 2.*xii*.1977, NMV-SD. 1♀ with pupal and larval exuviae, Tanjil R. at Old Tanjil, 24.*i*.1979, A. Glaister, emerged in lab. 26.*vii*.1979; 2♀♀, Chain Bay Stream, Mt. Butler, 8.*i*.1973, PZ; 10 L, Thomson R. sites (Appendix A), 25.*xi*.1976-2.*iii*.1978, NMV-SD; 26 L, Thomson R. sites (Appendix A), 27.*xi*.1979-29.*v*.1980, NMV-SD; 6 L, Caledonia R. below jn. of branches, 30.*xi*.1976-22.*ii*.1978, NMV-SD; 3 L, Dingo Ck, Caledonia R. track, 30.*xi*.1976, NMV-SD; 37 L, Macalister-Caledonia R.jn, 1.*xii*.1976-24.*ii*.1978, NMV-SD; 3 L, Snowy Ck, 8 km SE Mitta Mitta R., 10.*ii*.1978, 7.*iii*.1977, NMVSD; 15 L, Mitta Mitta R. sites (Appendix A), 6.*iii*.1977-15.*xi*.1977, NMV-SD; 1 L, Howqua R., 28.*ii*.1971, WDW; 1 L, Ovens R., east branch, 23.*ii*.1972, PZ; 1 L, Ovens R., 23.*ii*.1972, PZ; 1 L, Tawonga, 22.*ii*.1971, PZ; 1 L, Delatite R., 23.*vii*.1971, H.B.N. Hynes; 2 L, Yarra R., Milgrove S, 29.*x*.1979, J. Smith, CIT; 1 L, Latrobe R. at Hawthorn Ck jn, 1.*xii*.1978, P. Suter. NEW SOUTH WALES: 9♀♀, 4♂♂, Barrington House, via Salisbury, 7.*i*.1967, G. Monteith, QU; 1♀, with pupal and larval exuviae, Geehi R., 6.*i*.1973, PZ; 1 L, Geehi R., 7.*i*.1973, PZ; 1 L, Geehi R., Alpine Way, 6.*xi*.1973, PZ; 1 L, Snowy R, date?, PZ; 15 L, Upper Allyn R., 16.*ii*.1966, E.F. Riek, ANIC; 1 L, Michelong Ck, Wee Jasper, 25.*iv*.1963, E.F. Riek, ANIC; 1 L, Kiandra, 21.*ii*.1962, E.F. Riek, ANIC; 1 L, Cabboage Tree Ck, Canberra-Coast Rd, 7.*vii*.1965, E.B. Britton, ANIC.

Description

Female (Figures 3.66 - 3.68)

Total length 7.7 mm, head width 1.4 mm, pronotal length 1.5 mm, pronotal width 4.3 mm, width of pronotum between apical angles 1.9 mm, scutellar length 0.6 mm, scutellar width 0.7 mm, elytral length 6.1 mm, elytral width 5.0 mm.

General shape - Relatively large, broadly ovate beetle.

Head - Black, red ring around eye, pubescence parted along midline.

Pronotum - Medial region black with red patches, lateral regions red-brown. Medial region relatively glabrous, derm shining, minute punctures visible, lateral and basal regions with fine ashen pubescence. Region above scutellum with dense patch of ashen pubescence. Medial region gently convex, lateral regions wide, flattened. Lateral margins yellow, finely crenulate anteriorly.

Scutellum - Red-brown.

Elytra -Black with small irregular patches of red-brown. Region adjacent to scutellum black bordered by red-brown strip extending from anterior margin around to elytral suture. Dense fine pubescence over most of elytra plus some small clumps of coarse white pubescence, densest at basal third and apical third, bordering black, glabrous region, either side of suture, in middle third. Anterior medial region relatively glabrous, moderately shining, punctate with transverse wrinkles extending from elytral suture. Deep transerve marginal impression on lateral margin in basal third. Elytra swollen with greatest height attained at middle, greatest width at apical third. Striations visible laterally and apically. Margins yellow, wide.

Legs - Femur black, tibia brown, tarsi red-yellow.

Thorax - Pro- and mesosternum yellow, metasternum black, antecoxal piece yellow, metepisternum yellow.

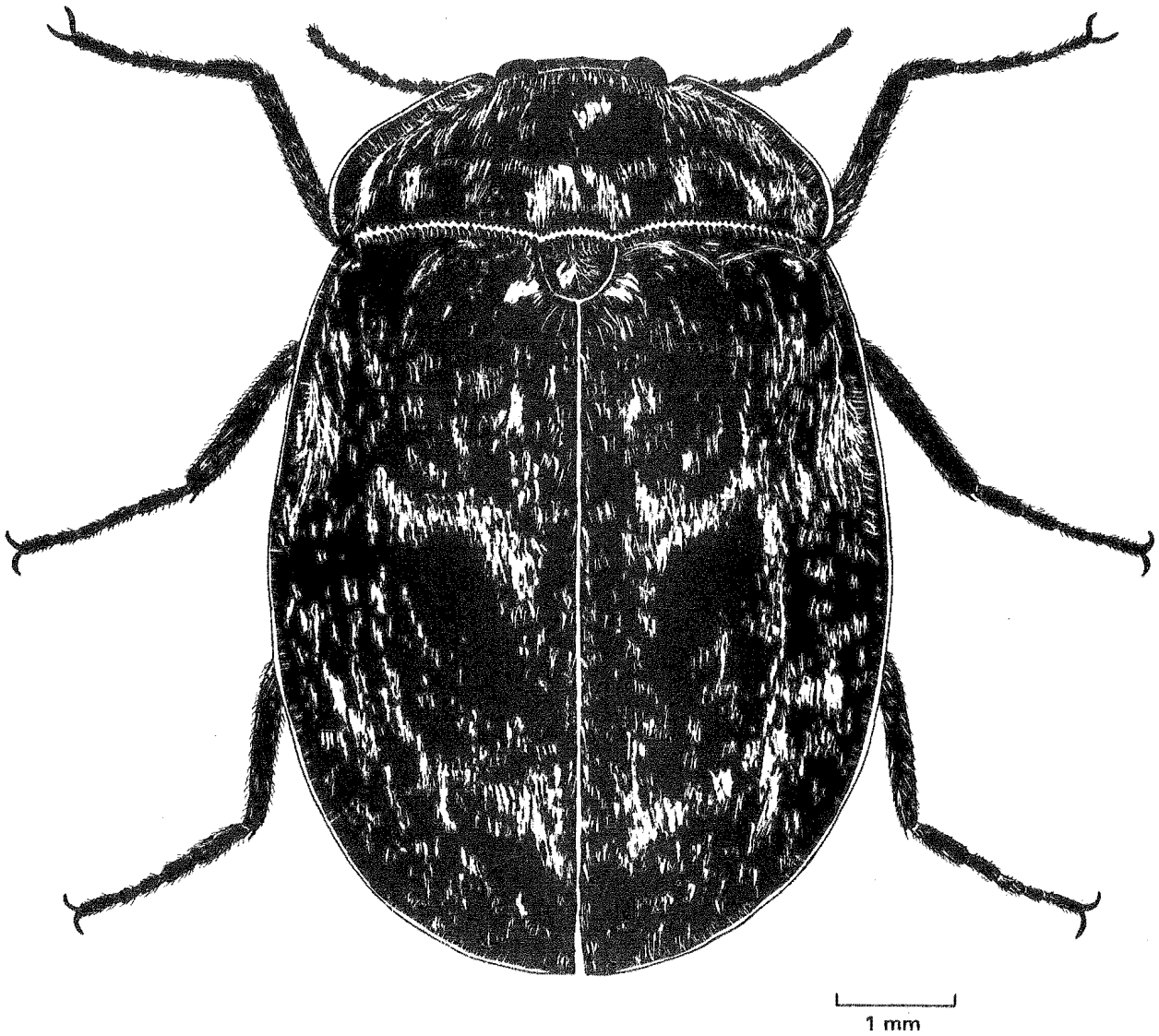


FIGURE 3.66 *Sclerocyphon zwicki*, ♀, holotype, dorsal view. Scale line = 1 mm.

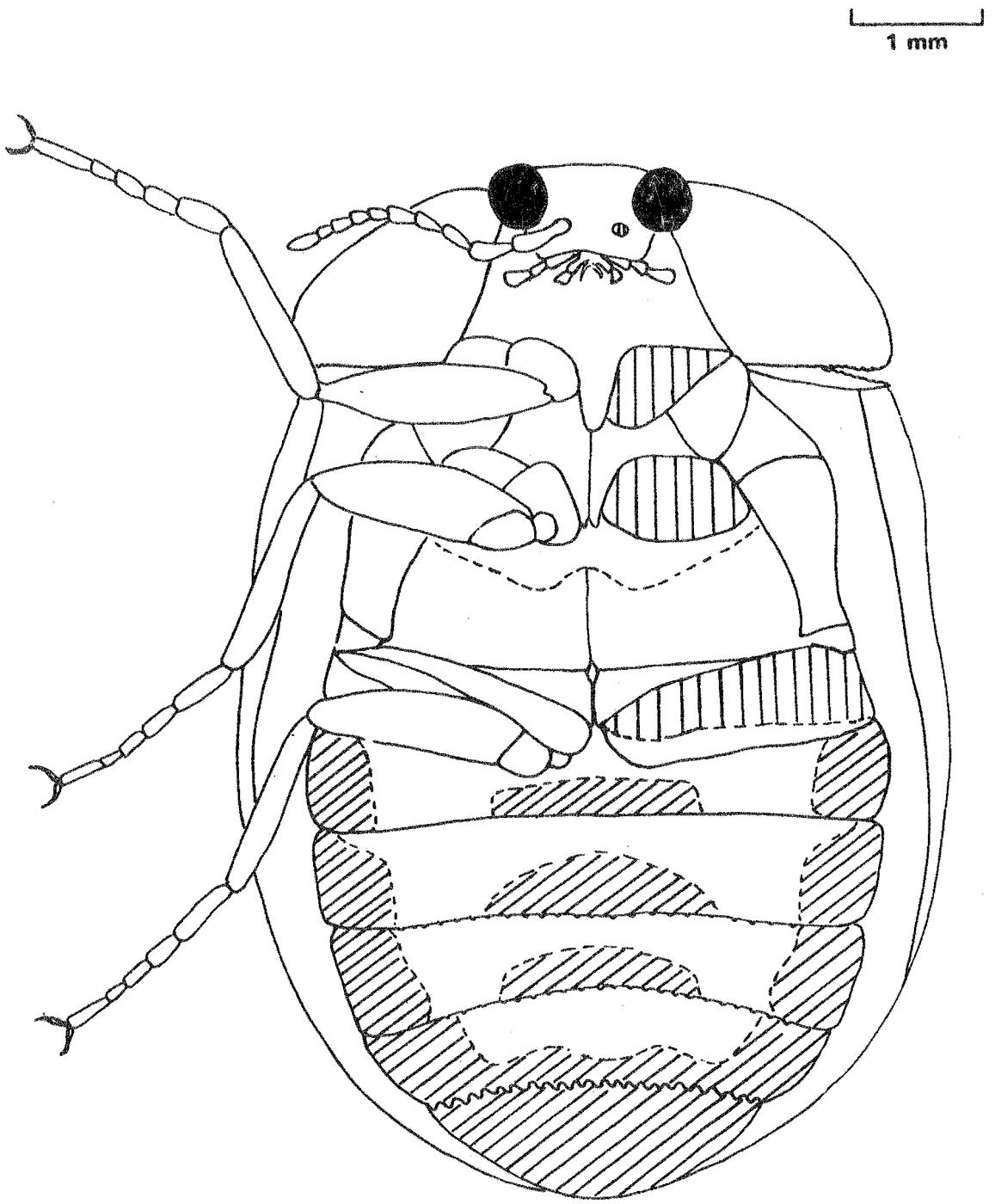
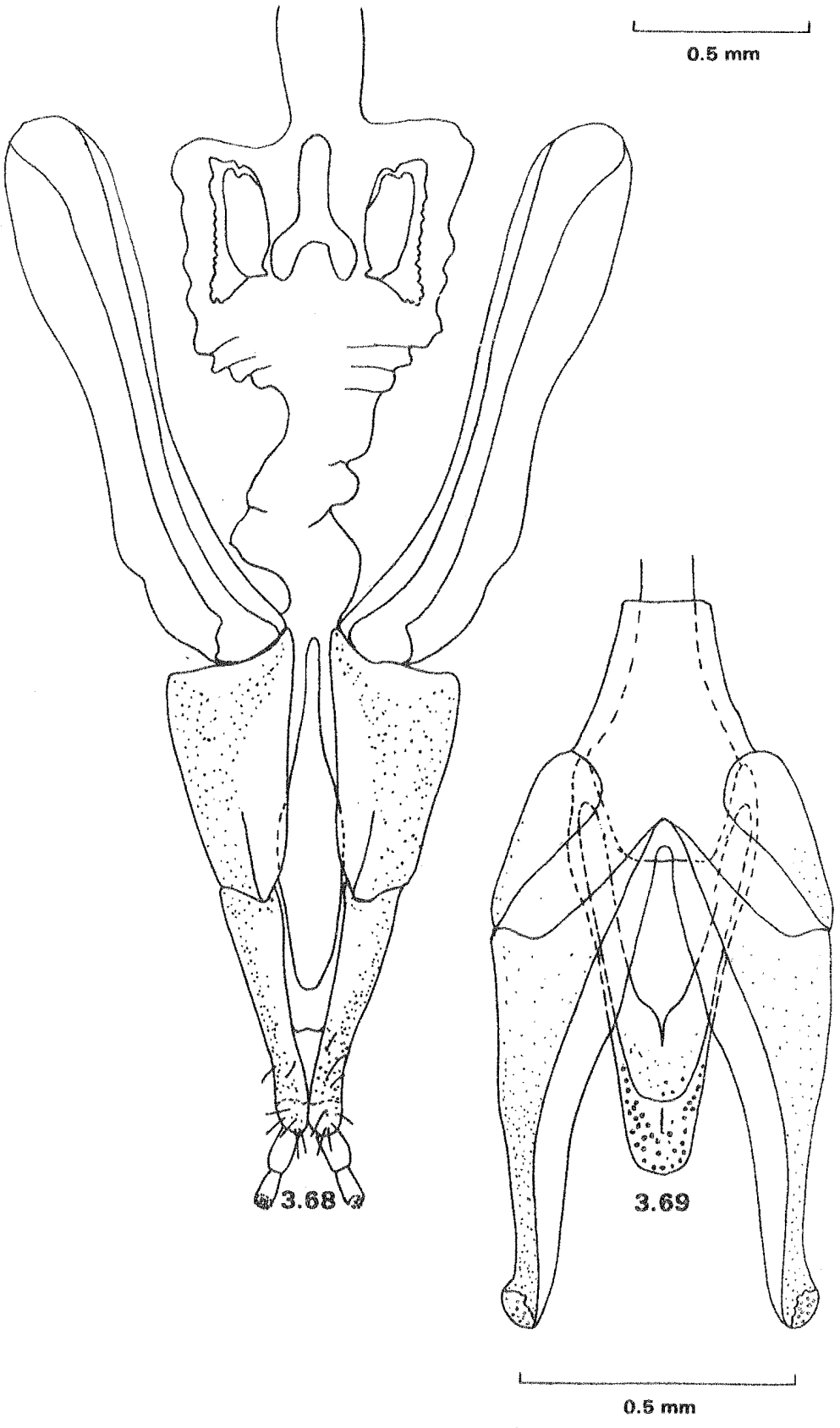


FIGURE 3.67 *Sclerocyphon zwicki*, ♀, holotype, ventral view. Scale line = 1 mm.



FIGURES 3.68-3.69 *Sclerocyphon zwicki:* (3.68) ♀, external genitalia, ventral view; (3.69) ♂, external genitalia, ventral view. Scale lines = 0.5 mm.

Abdomen - (Figure 3.67) - Segments 1-4 black laterally and medially, elsewhere yellow. Segment 5 black.

External genitalia (Paratype, Figure 3.68) - Pair of long, narrow hemisternites, punctate, setose distally, bearing 2-segmented styli. Sclerotised rod, embedded in vaginal wall between hemisternites, tapered anteriorly, expanded at middle, broad posteriorly. Pair of sclerotised plates, embedded in anterior dorso-lateral vaginal walls, long and narrow.

Male (Figure 3.69)

Total length 5.8 mm, head width 1.15 mm, pronotal length 1.3 mm, pronotal width 3.25 mm, width between apical angles of pronotum 1.45 mm, scutellar length 0.8 mm, scutellar width 0.5 mm, elytral length 4.4 mm, elytral width 3.85 mm.

Similar to female but smaller and with slight variations in colour and pubescence.

Pronotum - Mottled red-black, relatively glabrous.

Elytra - Basal medial region and strip each side of elytral suture red-brown. Lateral and apical regions black.

External genitalia (Paratype, Figure 3.69) - Aedeagus symmetrical, trilobate. Parameres long, thin, sclerotised, punctate with membranous tips. Dorsal sclerite of penis long and narrow with blunt apex, ventral sclerite much shorter.

Last instar larva (Figure 3.70, Pls 3.28-3.30)

Total length 8.5 mm, total width 6.2 mm, length of ninth tergite 1.7 mm, width of ninth tergite 1.6 mm.

General shape - Broad, nearly circular thoraco-abdominal shield, widest at tergite 2, decreasing in width to tergite 9.

Dorsal surface - Medial region dark brown with yellow patches on pro-, meso- and metanotum and tergites 1, 2, 7 and 8. Pronotum with two

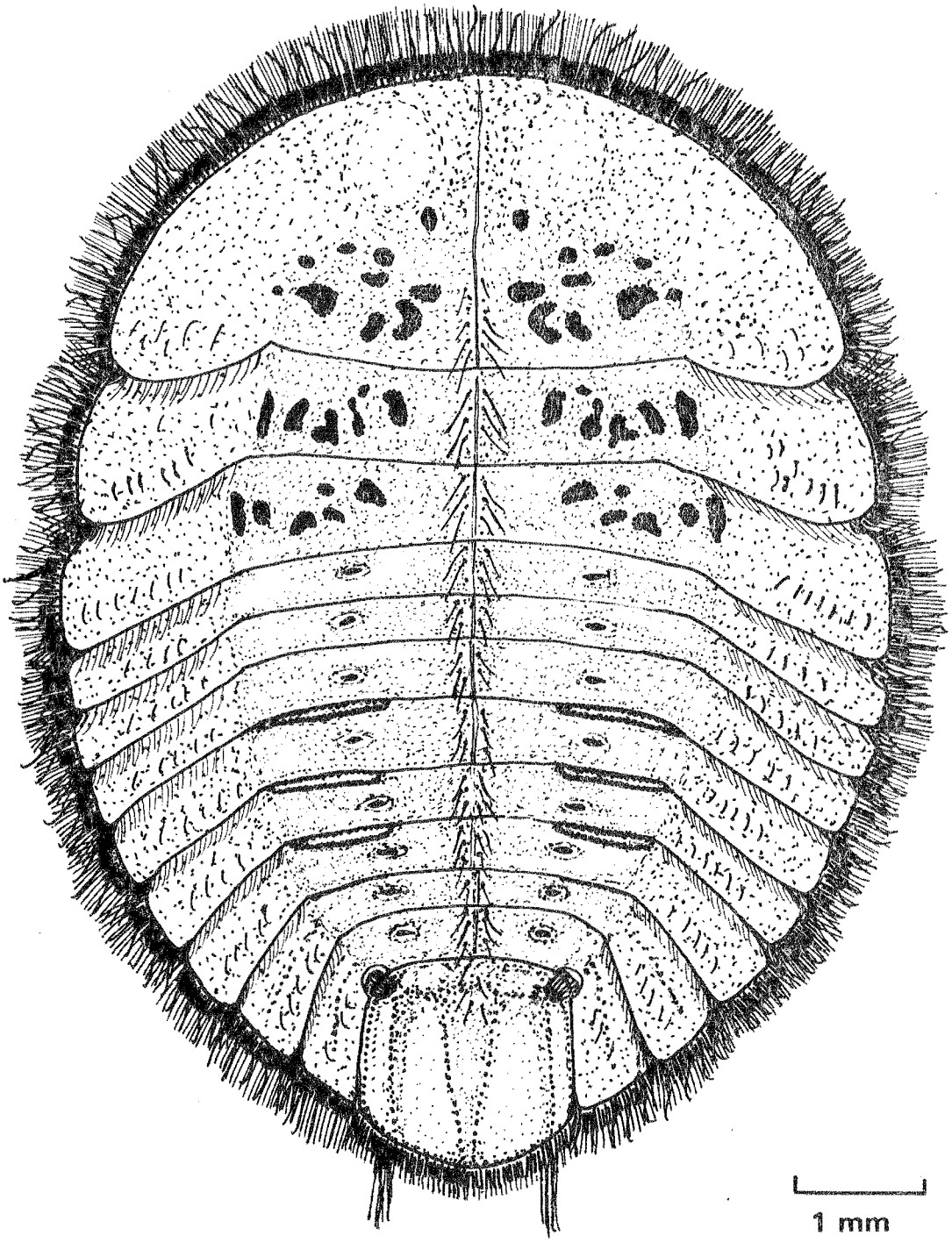
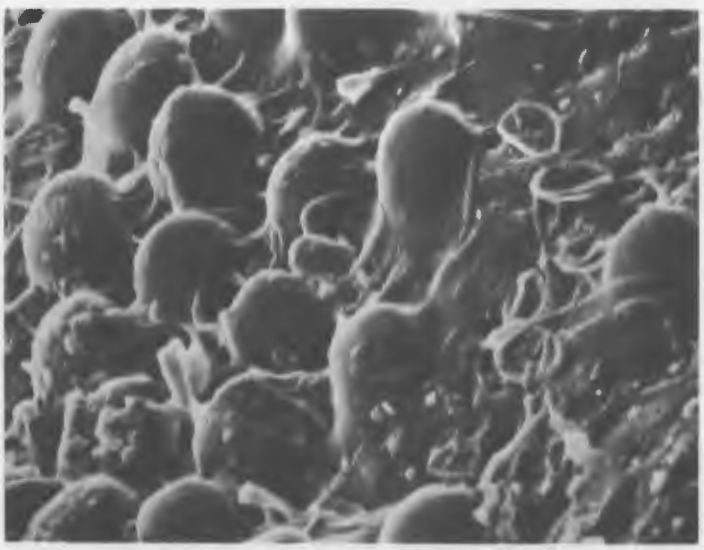


FIGURE 3.70 *Sclerocyphon zwicki*, last instar larva, paratype, dorsal view. Scale line = 1 mm.

3.28

3.29



3.30

PLATES 3.28-3.30 *Sclerocyphon zwicki*, last instar larva from Macalister-Barkly R jn, tergite 9: (3.28) x 40; (3.29) x 200, (3.30) x 650.

light patches over eyes, tergite 9 dark brown with ridges light brown, lateral laminae light brown. Entire medial region smooth and shining, possibly because of mucous secretions.

Entire marginal fringe of setae with 2 bands visible, narrow, yellow inner band made up of stiff inner section of each seta, wider, transparent outer band where seta soft, flexible, tapering to minute point. Overlying this fringe an irregular fringe of dark brown, randomly orientated setae, slightly longer than underlying fringe. Trailing edge of all laminae with fringe of fine, transparent setae.

Extremely minute sclerotised cuticular beads present on medial region, lateral laminae with relatively large, dark, rounded cuticular beads scattered randomly over surface plus a transverse row extending across laminae of tergites 5, 6, 7 and 8.

Very fine pores scattered over medial region. Long black setae, usually posteriorly directed, sometimes randomly orientated, extending from pores in longitudional row, on each side of midline, on each thoracic and abdominal segment.

Pro-, meso and metanotum and tergites 1-8 with transverse row of short black setae extending across lateral laminae. Extra setae, anterior to this row, on pro- and mesonotum.

Pronotum with 5 pairs of irregular pits, 4 pairs of circular pits arranged in a semi-circle, and 1 pair of anterior pits. Meso- and metanotum with 6 pairs of irregular pits. All pits dark.

Three pairs of gin traps present on adjoining margins of tergites 3-4, 4-5, 5-6. All pairs wide with both upper and lower edges thickly sclerotised. The corresponding regions on posterior margin of tergite 6 sometimes sclerotised, creating a pair of "half" gin traps.

Tergite 9 (Pls 3.28-3.30) with an upraised, shining central ridge, outlined by cuticular beads, plus lesser lateral ridges. Central ridge tapering from anterior to posterior margin. Lateral margins straight,

posterior margin produced in regular semi-circle, tergite with rectangular outline overall. Posterior margin with regular fringe plus two groups of longer setae extending from margin either side of medial region.

Diagnosis

Adults can be distinguished by the following combination of characters; relatively large size, broad ovate body, "velvety" rather than shining dorsal surface, elytral striations visible laterally and apically, and a long narrow dorsal penile sclerite or narrow elongate vaginal plates.

Larvae can be distinguished by the following combination of characters; 3 gin traps, tergite 9 with its nearly rectangular outline and shining, upraised central ridge, broad, ovate, sometimes circular thoraco-abdominal shield, shining medial region, and two longitudinal rows of black setae, one each side of the midline.

Comments

The specific epithet was chosen to honour Dr. P. Zwick who first recognised the existence of this species. Dr. Zwick made his collection of Australian psephenid material available for study in 1979 and it contained a beetle of this species, together with its pupal and larval exuviae, collected from the Geehi River in 1973.

I had first observed the distinctive larva of this species amongst psephenid material from the Gippsland rivers, in the National Museum of Victoria Survey Department collection, in 1978. To associate larva and adult, live larvae were held in the laboratory and the successful emergence of one beetle, only, occurred in 1979.

Both adults and larvae are large relative to most other species of *Sclerocyphon*. Two different forms of the larval shield have been observed;

the wide almost circular form described here, and a more elongate, oval form.

Present distribution records indicate that this species is restricted to fairly high altitudes in eastern Victoria and New South Wales.

Sclerocyphon type A

(Figure 3.71, Pls 3.31 - 3.33)

Material Examined

Voucher specimens - QUEENSLAND: 23 L, Little Mulgrave R., 28.*vi*.1971, E.F. Riek, ANIC.

Other material examined - QUEENSLAND: 12 L, Beatrice R., Palmerston Hwy, 30.*vii*.1956, T.E. Woodward, QU; 3 L, Little Mulgrave R., 28.*vi*.1971, E.F. Riek, PZ; 14 L, Fishery Falls, S of Gordonvale, 29.*vi*.1971, E.F. Riek, ANIC; 18 L, Freshwater Ck, nr Redlynch, 25.*x*.1966, E.B. Britton, ANIC; 6 L, Freshwater Ck, 6 mi S of Redlynch, 25.*x*.1966, E.B. Britton, ANIC; 1 L, "The Boulders", W of Babinda, 29.*vi*.1971, E.F. Riek, ANIC; 7 L, Behana Gorge, nr Gordonvale, 15 mi S of Cairns, Feb.1973, PZ; 24 L, Little Beatrice R. at McHugh Bridge, Palmerston National Park, Feb.1973. PZ.

Description

Last instar larva (Figure 3.71, Pls 3.31 - 3.33)

Total length 8.75 mm, total width 6.2 mm, length of ninth tergite 1.5 mm, width of ninth tergite 1.5 mm.

General Shape - Broadly circular thoraco-abdominal shield, widest at metanotum, decreasing in width from tergite 4 to 9.

Dorsal surface - Medial region brown, lateral laminae yellow. Pronotum with two light patches above eyes. Tergite 9 brown with ⊐-shaped yellow region.

Entire marginal fringe of setae with two bands visible; narrow, brown inner band wider, transparent outer band where setae soft, flexible, tapering to minute point. Overlying this fringe an irregular fringe of dark brown, randomly orientated setae, slightly longer than setae of regular fringe. Trailing edge of all laminae with fringe of fine, transparent setae.

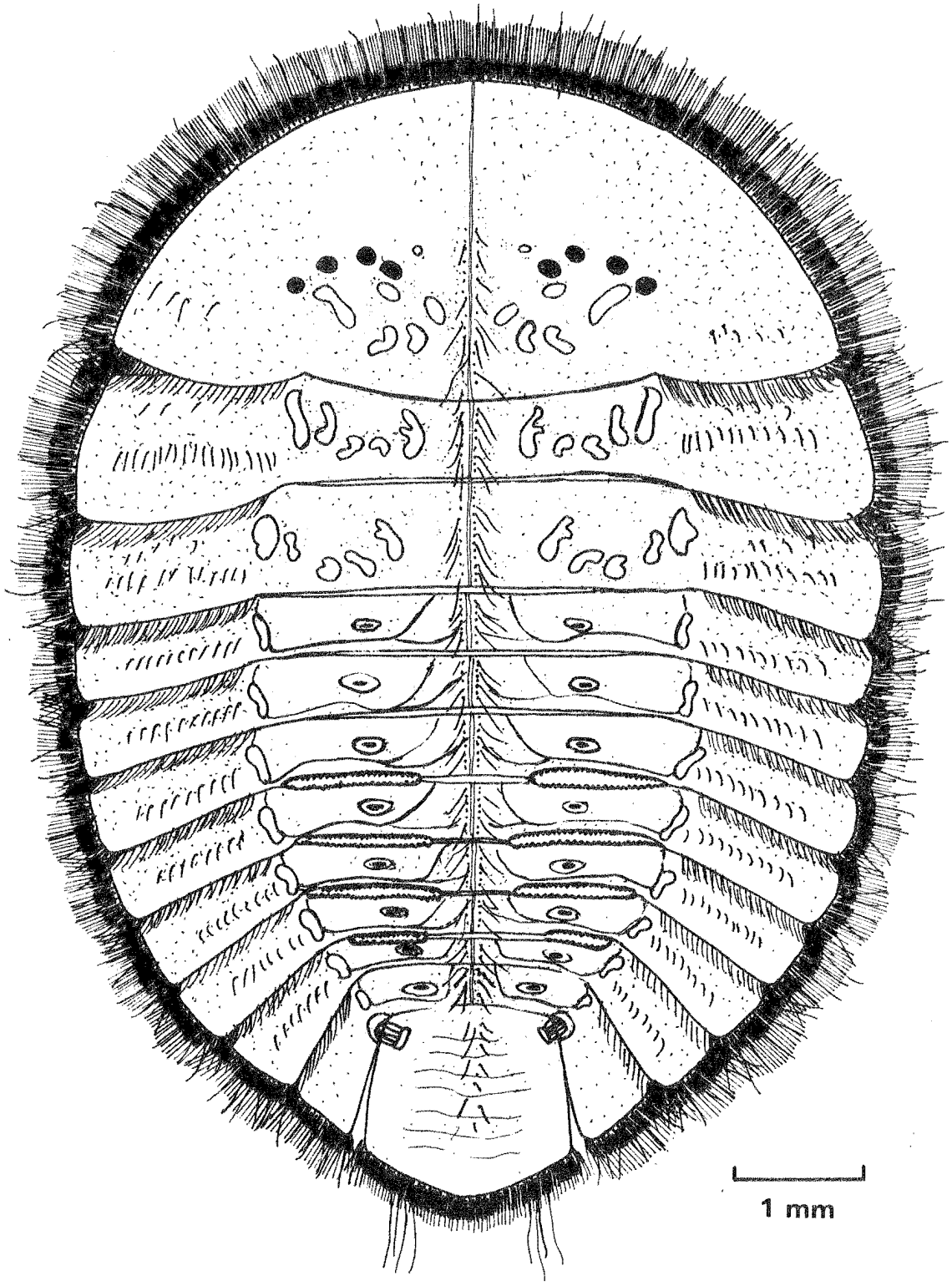
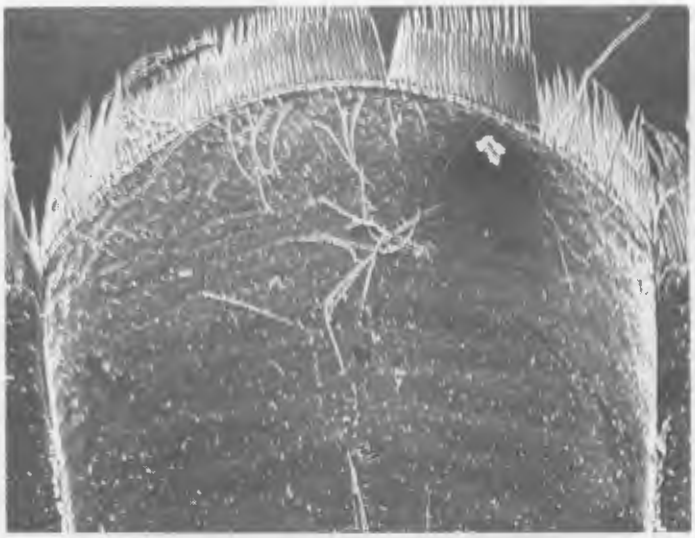
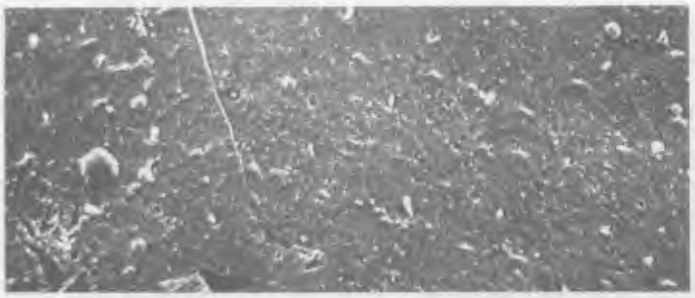


FIGURE 3.71 *Sclerocyphon* type A, last instar larva from Little Mulgrave R, dorsal view. Scale line = 1 mm.

3.31



3.32



3.33

PLATES 3.31-3.33 *Sclerocyphon* type A, last instar larva from Little Mulgrave R; (3.31) tergite 9,x 40; (3.32) tergite 9 x 200; (3.33) long setae each side of mid-dorsal line on tergite 4, x 100.

Uniform covering of very small dark, sclerotised cuticular beads on lateral laminae and anterior region of pronotum, beads absent from medial region.

Pores scattered across entire shield, densest in medial region. Medial region smooth, shining, possibly because of mucous secretions.

Long black setae (Pl. 3.33) posteriorly directed, extending from pores in longitudinal row, on each side of midline, on each thoracic and abdominal segment. Short black setae (fine branching visible with scanning electron microscopy) in transverse row across lateral laminae of meso- and metanotum and tergites 1-7. Meso- and metanotum with extra setae, anterior to transverse row, as well.

Pronotum with 5 pairs of irregular pits, 4 pairs of circular pits (usually dark) and one anterior pair. Meso- and metanotum with 6 pairs of irregular pits. Most pits light coloured, all without border of beads present in other species.

Tergites 1-8 with upraised, transverse region, surrounding ecdysial scar, outlined by "wrinkles" or folds in cuticle, each side of midline. Junction of body and lateral lamina with sloping longitudinal pit.

Four pairs of gin traps present on adjoining margins of tergites 3-4, 4-5, 5-6 and 6-7. Three anterior pairs wide, extending most of way across body, posterior pair narrower.

Tergite 9 (Pls 3.31, 3.32) lacking upraised longitudinal ridges. Entire tergite smooth, shining, possibly due to mucous secretion from numerous pores scattered over surface. Few cuticular beads visible but cuticle with many transverse "wrinkles" or folds. Nearly square outline, posterior margin produced in shallow regular semi-circle, lateral margins straight, sloping slightly outwards. Posterior margin with regular fringe plus two groups of longer, dark setae, extending from margin on each side of middle.

Diagnosis

Larvae of this type can be distinguished by the following combination of characters; 4 gin traps, broad, circular or oval dorsal shield, longitudinal row of setae dorsally, each side of midline, transverse row of setae on lateral laminae, dorsal medial region shining and lacking cuticular beads, longitudinal pits at junction of each lateral lamina and body, and nearly square tergite 9, lacking ridges but with fine transverse folds.

Comments

Larvae of this type are the most distinctive of all larval *Sclerocyphon*, possessing a number of features that are either unique or present in only one other species, *S. zwicki*.

This type has been recorded only from the Cairns-Atherton district of north Queensland. This restricted distribution together with the wide body form suggests that it may be the larval form of *S. aquilonius* (a very broad beetle).

Sclerocyphon type B

(Figure 3.72, Pls 3.34 - 3.39)

Material Examined

Voucher specimens - QUEENSLAND: 10 L, creek at Buderim, on S facing slope below Nambour-Maroochydore Hwy, 2.*ii*.1980, J.A. Smith, B. Smith, NMV; 26 L, same data, held by J.A. Smith.

Other material examined - QUEENSLAND: 8 L, Brisbane, 15.*vi*.1955, Kirkpatrick, QU; i L, Timbeerwah Falls, 5 km W of Tewantin, 12.*iv*.1979, H.B.N. Hynes; 2 L, Woondum Ck, 1.5 km SW of Mt. Boulder, 14.*iv*.1979, H.B.N. Hynes; 11 L, Alice R., Townsville, date? Coll? JCUNQ; 3 L, 2 km N Hartley Ck, 17.*vi*.1971, E.F. Riek, PZ; 1 L, Lamington National Park, 29.*viii*.1958, Coll?, QU.

Description

Last instar larva (Figure 3.72, Pls 3.34 - 3.39)

Total length 6.6 mm, total width 3.4 mm, length of ninth tergite 1.0 mm, width of ninth tergite 1.4 mm.

General shape - Narrow, elongate thoraco-abdominal shield, widest at metanotum, tapering to tergite 9.

Dorsal surface - Medial region dark brown, tergites 2, 3, 5 and 6 with yellow patch at each side of body, tergites 7 and 8 with yellow patch at centre. Pronotum with light patch above each eye. Lateral laminae pale yellow. Tergite 9 completely dark.

Entire marginal fringe of setae with 2 bands visible; a wide, regular, stiff, inner section, and a narrow, transparent outer section where setae soft, flexible, tapering to a minute point.

Pro-, meso- and metanotum with dark, pointed, sclerotised cuticular beads around pored regions and pits and extending across anterior shield

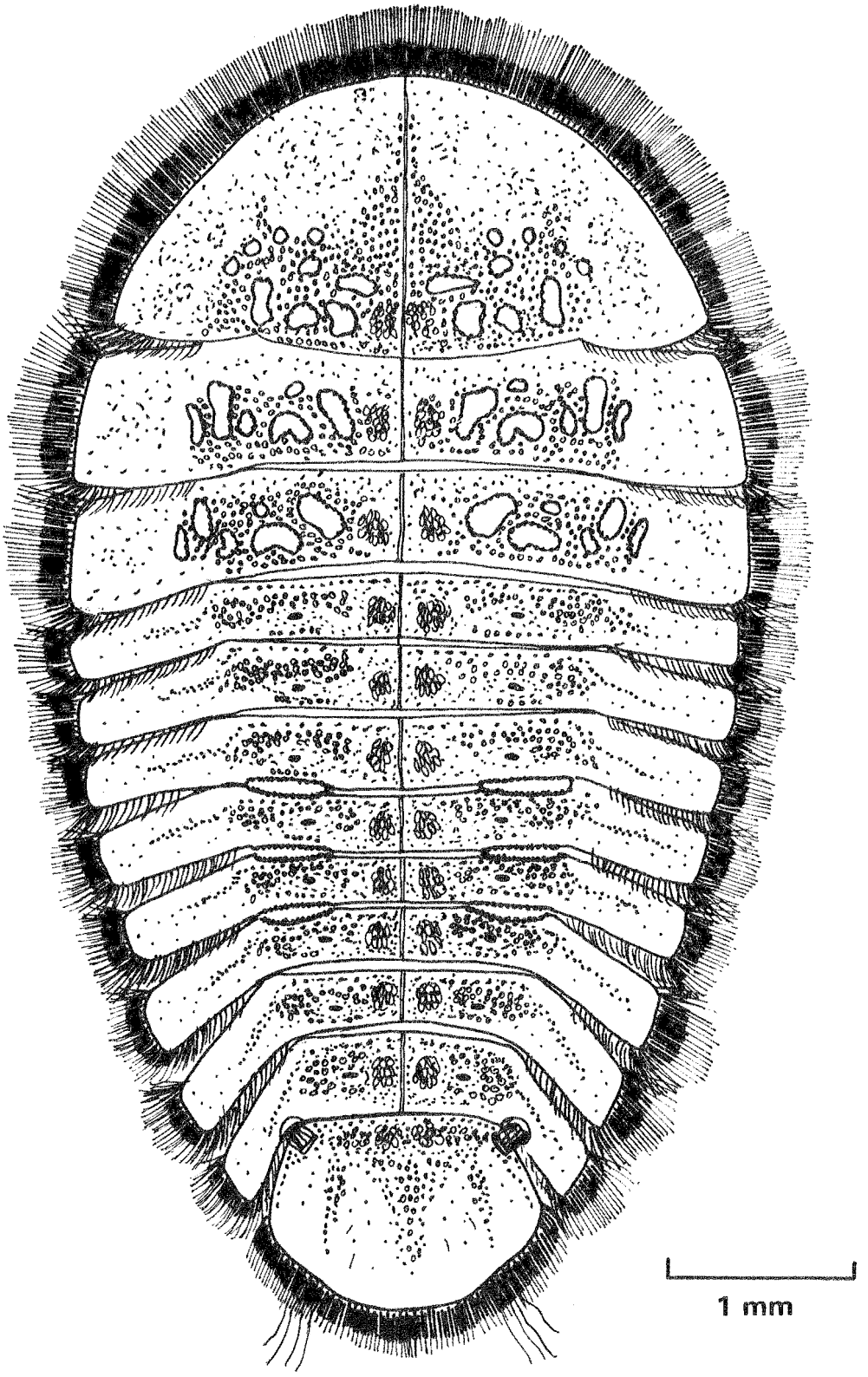
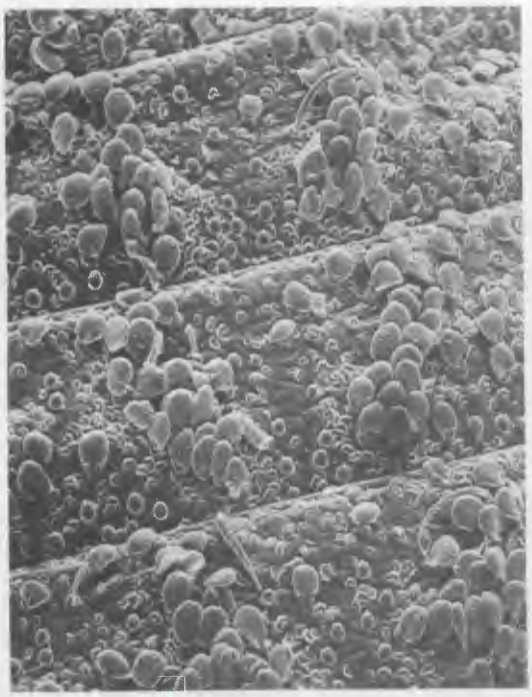
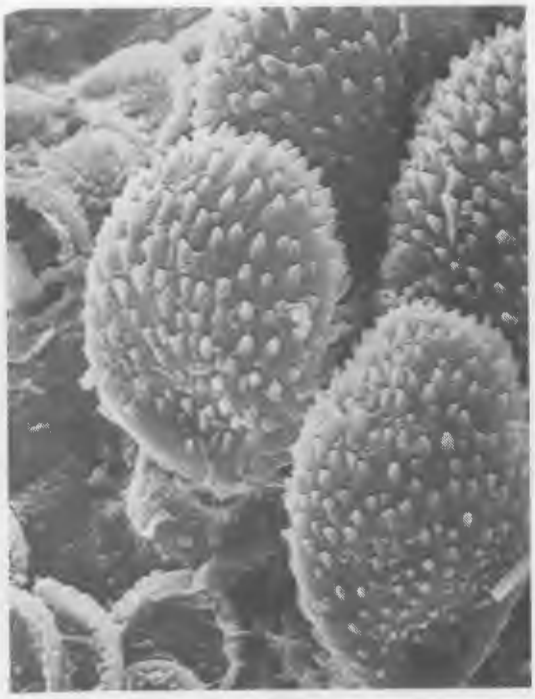


FIGURE 3.72 *Sclerocyphon* type B, last instar larva from Buderim Ck, dorsal view. Scale line = 1 mm.



3.34

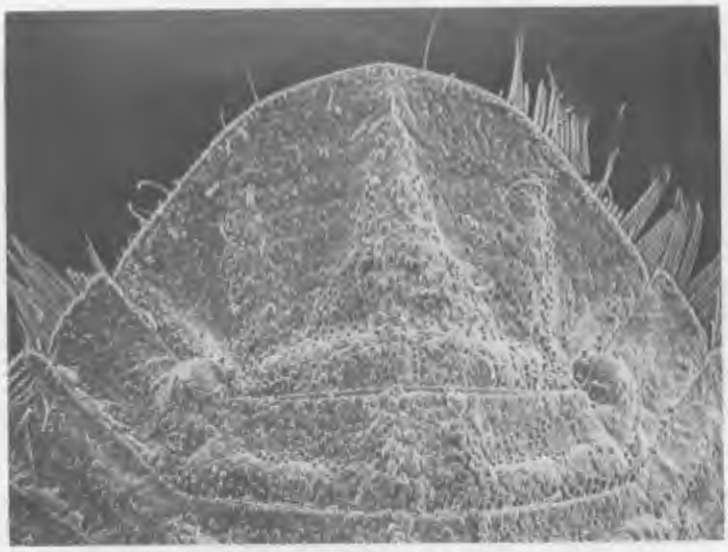


3.35

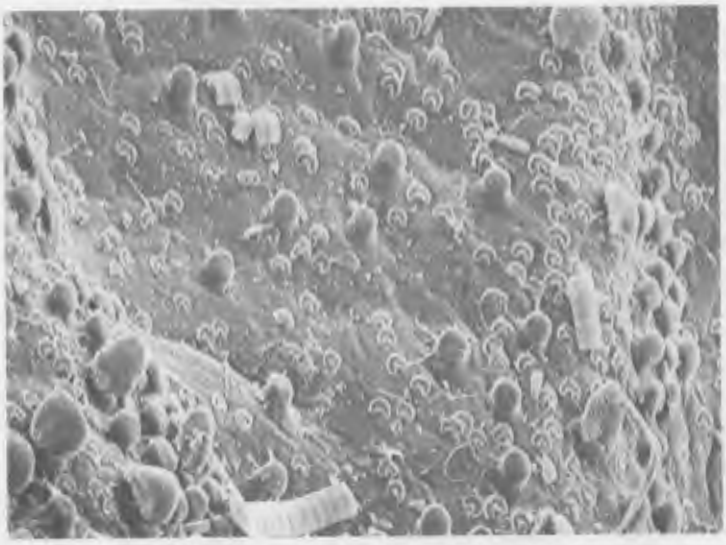
3.36

PLATES 3.34-3.36 *Sclerocyphon* type B, last instar larva from Buderim Ck; (3.34) clumps of mucous-coated trichoid sensilla in mid-dorsal region of tergites 5, 6 and 7, x 120; (3.35) mucous-coated trichoid sensilla , x 1000; (3.36) mucous-coated trichoid sensilla and cuticular beads on tergite 5, x 500.

3.37



3.38



3.39

PLATES 3.37-3.39 *Sclerocyphon* type B, last instar larva from Buderim Ck, tergite 9: (3.37) x 40; (3.38) x 200; (3.39) x 650.

of pronotum, laminae of meso- and metanotum. Tergites 1-8 with two rows of beads across medial region, one row anteriorly, the other posteriorly. Anterior row extending down each lateral lamina to middle, beads densest at junction of body and lamina, sparser at middle, some smaller beads scattered around edge of lamina.

Pores scattered over entire shield, densest beneath shining grey mucus between pits and along midline on pronotum. Also between pits on meso- and metanotum and on upraised transverse strip above ecdysial scar, each side of midline on tergites 1-8. Some pores with mucus-coated trichoid sensillae, others with hairs, best seen by scanning electron microscopy (Pls 3.34 - 3.36).

Twelve paired groups of trichoid sensilla in medial region, one group to each side of midline on each thoracic and abdominal segment. Groups with shining, grey appearance beneath light microscope, discrete spathulate sensilla with ornate muco-polysaccaride coat visible with scanning electron microscopy (Pls 3.34, 3.35).

Pronotum with 5 pairs of irregular pits and 4 pairs of circular pits. Meso- and metanotum with 6 pairs of irregular pits. All pits light coloured and bordered by beads.

Three pairs of gin traps present on adjoining margins of tergites 3-4, 4-5, 5-6. Two anterior pairs slightly wider than posterior pair. Lower margin of each gin trap heavily sclerotised, upper margin only weakly sclerotised.

Tergite 9 (Pls 3.37 - 3.39) with upraised, tapered, central ridge extending to middle plus a lesser ridge on each side, all outlined by cuticular beads. Anterior margin upraised with dense row of cuticular beads. Beads sparse between ridges and at posterior margin. Pores on central ridge with trichoid sensilla (visible with scanning electron microscopy). Posterior margin with slight concave sinuosity each side of rounded apex, some specimens with pointed apex. Lateral margins short,

curved outwards. Posterior margin with regular fringe plus two groups of longer setae, one each side of middle.

Diagnosis

Larvae of this type can be distinguished by the following combination of characters; 3 gin traps, tergite 9 with 3 ridges not extending beyond middle and outlined by beads, transverse rows of cuticular beads across body and lateral laminae on tergites 1-8, and spathulate trichoid sensilla with ornate muco-polysaccaride coating present in mid-dorsal clumps as well as scattered randomly over entire shield.

Comments

This larval type undoubtedly represents a new species of *Sclerocyphon* but as yet the larva has not been associated with its adult, despite attempts to rear adults in the laboratory from larvae taken from Buderim Creek.

Present records indicate that this type occurs only in Queensland, on the coastal strip from Lamington National Park to Townsville, although further collecting may extend this range.

The possession of 3 gin traps and the form of tergite 9, with its 3 ridges, places this larval type within the *S. striatus* species-group. However the larvae are easily distinguished from all others in the group by both the distinctive patterns of the cuticular beads and the unusual decoration of the trichoid sensilla .

Possibly the heavier coating of mucus on the dorsal surface and the unique form of the mucus-coated trichoid sensilla have developed in response to warm stream temperatures. Larvae of this type inhabit very warm coastal streams, the water temperature at Buderim Creek, when larvae were collected in February, 1979, was 24°C at 9 a.m.

Sclerocyphon type C

(Figure 3.73, Pls 3.40 - 3.44)

Material Examined

Voucher specimens - QUEENSLAND: 3 L, Malaan, 2000 ft, N. Queensland, T.E. Woodward, QU.

Other material examined - QUEENSLAND: 1 L, Highvale, 9.*v*.1959, C.L. Smith, QU; 10 L, Highvale, nr Mt. Glorious, 30.*iii*.1955, F.A. Perkins, QU; 1 L, First creek past aboriginal settlement before Mossman Gorge, 14.*viii*.1979, A. Bubenicek; 4 L, Mossman Gorge, 14.*viii*.1979, A. Bubenicek; 1 L, Creek between Cooper Ck and Hutchinsons Ck, Cape Tribulation Rd, 13.*viii*.1979, A. Bubenicek; 5 L, Reliance Ck, Mackay, 17.*viii*.1978, JCUNQ; 16 L, South Johnstone R, 28.*ix*.1976, JCUNQ; 4 L, North Johnstone R, 25.*ix*.1976, JCUNQ: 1 L, Millstream Falls, W of Ravenshoe, 25.*vi*.1971, E.F. Riek, PZ; 1 P, 9 L, Iron Range, Mt. Tozer foothills, 4.*vi*.1971, E.F. Riek, PZ; 1 L, 16 km on Davies Ck Rd, E of Mareeka, 18.*vi*.1971, E.F. Riek, PZ; 12 L, Ugly Gully Ck, Mt. Crosby, nr Brisbane, date?, Coll?, PZ; 2 L, Beatrice R, Palmerston National Park, 27.*vi*.1971, E.F. Riek, PZ; 7 L, Mossman Gorge, 12.*vi*.1971, E.F. Riek, ANIC; 1 L, Crystal Ck, 23 mi. SSE Ingham, 10.*xii*.1968, E. Britton, ANIC; 2 L, "The Boulders" W of Babinda, 29.*vi*.1971, E.F. Riek, ANIC; 3 L, Creek nr Julatten Station, Mossman-Mt. Lewis Rd, 1200 ft, 30.*x*.1966, E. Britton, ANIC; 4 L, Behana Gorge, S of Gordonvale, 29.*vi*.1971, E.F. Riek, ANIC; 7 L, Tinaroo Dam, 2 km on Mt. Edith Rd, 23.*vi*.1971, E.F. Riek, ANIC; 3 L, Upper Lanelly Ck, Coen district, Cape York Peninsula, 10-11.*xi*.1971, S.R. Monteith, ANIC; 12 L, Finch Hatton, 1.*vii*.1971, E.F. Riek, ANIC; 7 L, Behana Gorge, nr Gordonvale,Feb.1973, PZ; 3 L, Cunninghams Gap, 24.*iii*.1963, C. Watts. NEW SOUTH WALES: 21 L (20.*xi*.1978), 1 L (6.*x*.1978), 1 L (23.*x*.1976), 57 L (6.*x*.1978), 2 L (20.*xi*.1978), 2 L (25.*xiii*.1976), 12 L (6.*x*.1978) all in freshwater turtle gut contents, Georges Ck at

"Murrungi" on Kempsey-Armidale Rd, 80 km SE Armidale.

Description

Last Instar Larva (Figure 3.73, Pls 3.40-3.44)

Total length 6.4 mm, total width 4.1 mm, length of ninth tergite 1.1 mm, width of ninth tergite 1.2 mm.

General shape - Broadly ovoid thoraco-abdominal shield, widest at tergite I, tapering gently to tergite 9.

Dorsal surface - Medial region brown, lateral laminae pale yellow, some evidence of bleaching of colour, possibly due to length of time of preservation in alcohol (approximately 25 years).

Entire marginal fringe of setae with two bands visible; broad, regular, yellow stiff inner section, and narrow outer section where setae soft, transparent, flexible, tapering to minute point, some setae broken. Trailing edge of all laminae with fringe of fine, soft setae.

Uniform covering of small, brown, sclerotised cuticular beads over body. Dark dense cluster of beads at junction of body and lateral laminae. Beads absent from shining pored regions on tergites. Lateral laminae with beads largest and densest at anterior margin, smaller, sparser posteriorly.

Pores visible between pits on pro-, meso- and metanotum. Pores visible, beneath shining yellow mucus, on two upraised transverse patches above ecdysial scar, each side of midline, on tergites 1-8 (Pls 3.40, 3.41).

Twelve paired groups of trichoid sensilla in medial region, one group to each side of midline on each thoracic and abdominal segment. Discrete sensilla , visible only with scanning electron microscopy, often broken, (Pl. 3.41). Beneath light microscope each group visible as shining grey mucus-coated mass, on small swelling, fairly widely

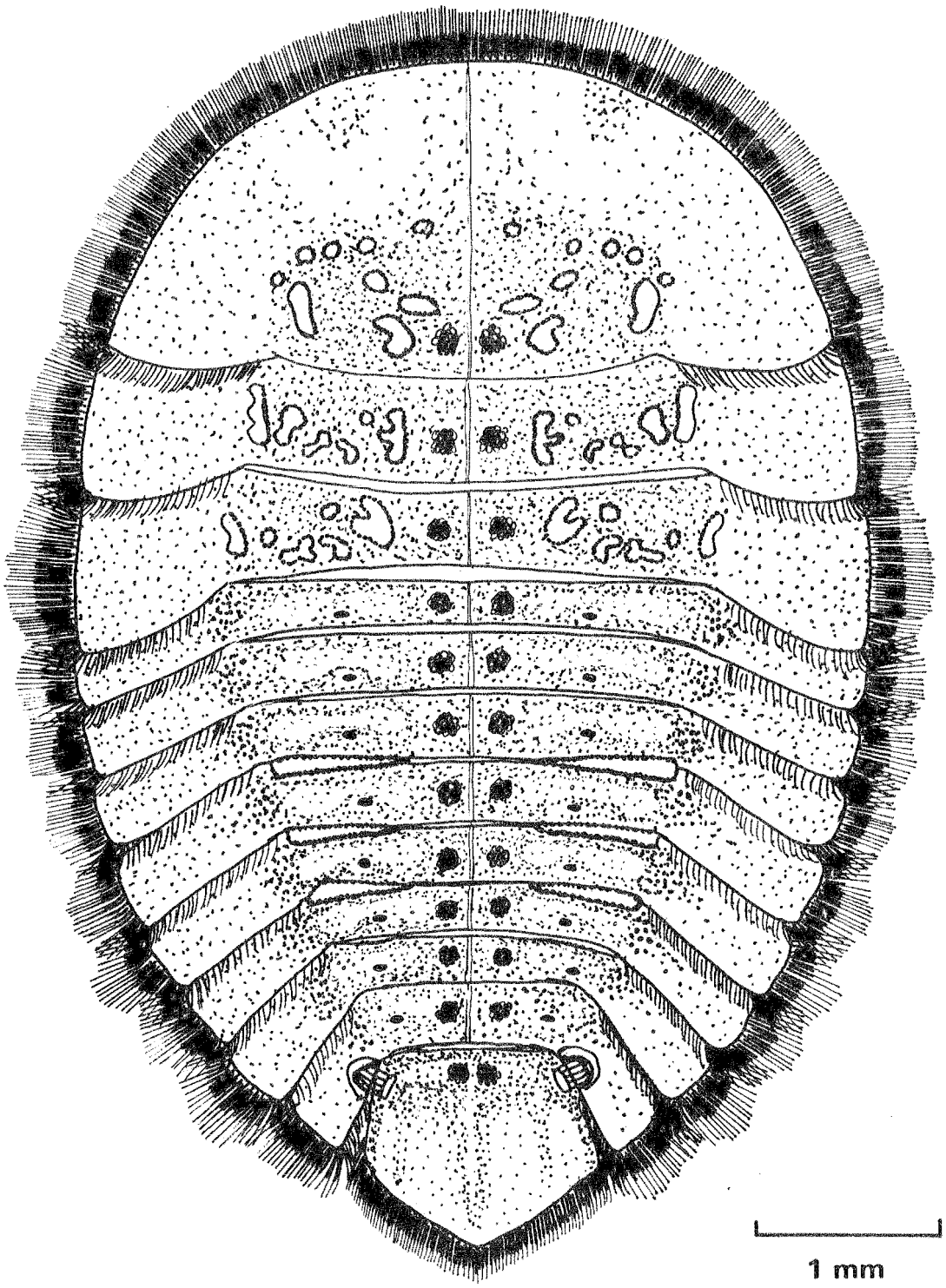
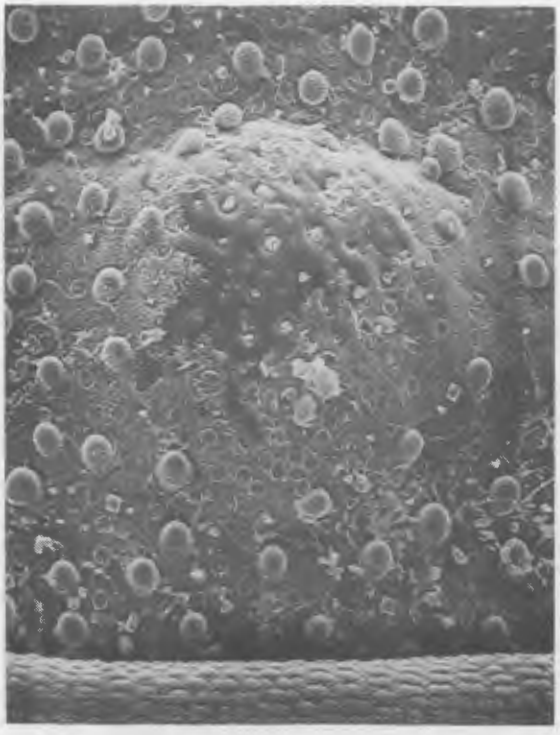


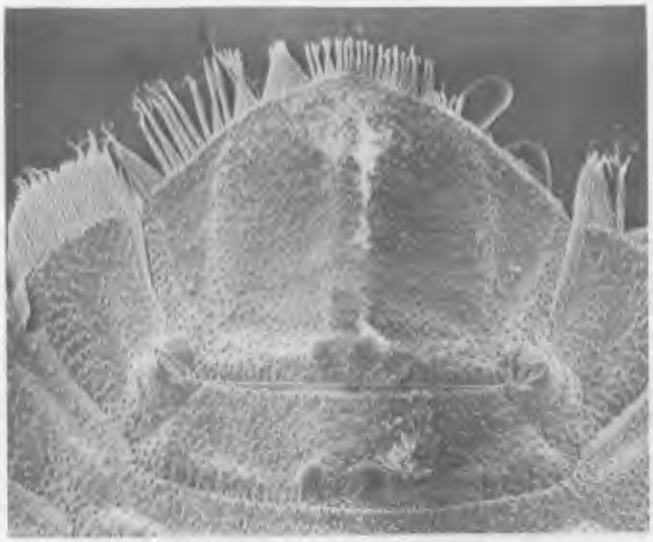
FIGURE 3.73 *Sclerocyphon* type C, last instar larva from Malaan, dorsal view. Scale line = 1 mm.

3.40



3.41

PLATES 3.40-3.41 *Sclerocyphon* type C, last instar larva from Malaan: (3.40) upraised transverse ridges and upraised mid-dorsal regions (trichoid sensilla mostly abraded) on tergites 3, 4, 5, 6, 7 and 8, x 40; (3.41) upraised region with remnants of abraded trichoid sensilla in pores, x 250.



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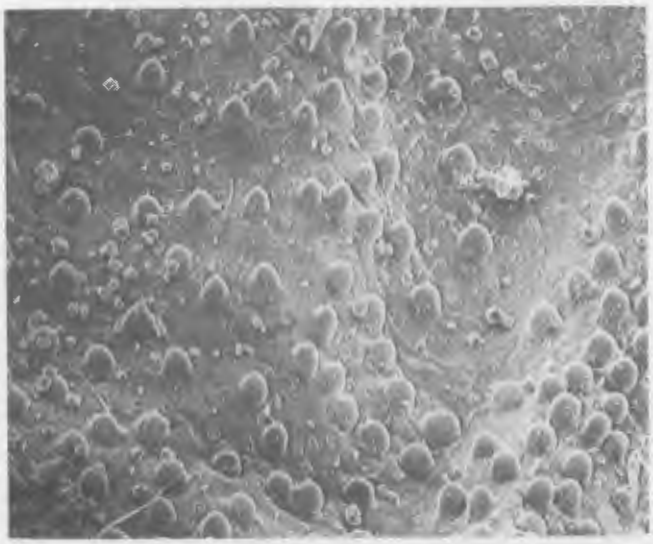
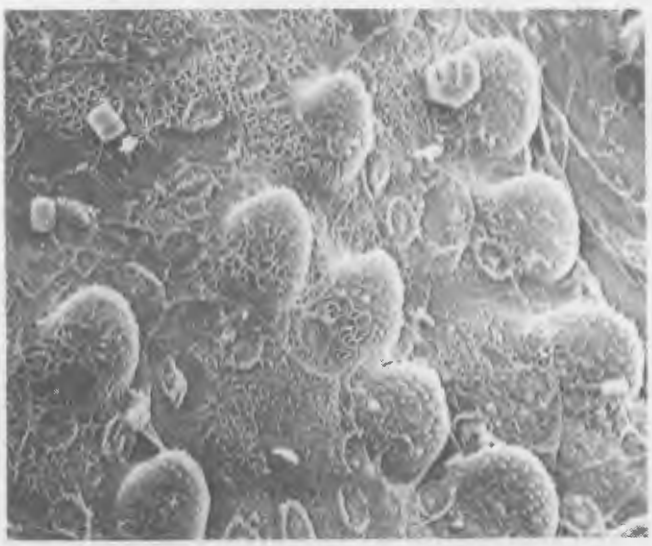


3.43



3.44

PLATES 3.42-3.44 *Sclerocyphon* type C, last instar larva from Malaan, tergite 9: (3.42) x 40; (3.43) x 200; (3.44) x 650.

separated, each side of midline. Some pores visible beneath mucus.

Pronotum with 5 pairs of irregular pits, 4 pairs of circular pits and one anterior pair. Meso- and metanotum with 6 pairs of irregular pits. All pits light coloured and bordered by beads.

Three pairs of gin-traps present on adjoining margins of tergites 3-4, 4-5, 5-6. Two anterior pairs wide, posterior pair narrower.

Tergite 9 with narrow, upraised central ridge extending to posterior margin, a lessor ridge on each side. Three ridges densely beaded, anterior and lateral margins with dense row of beads, area between ridges and posterior region with sparser, smaller beads. Posterior margin with pointed, or rounded apex, a slight sinousity each side at culmination of side ridges. Lateral margins slightly curved, sloping outwards.

Diagnosis

Larvae of this type can be distinguished by the following combination of characters; 3 gin traps, the form of tergite 9 with its narrow central ridge and pointed or rounded apex, and the small, upraised, medial groups of trichoid sensilla .

Comments

The distribution of this larval type extends from the Coen district on Cape York Peninsula, the northernmost tip of eastern Australia, to the Kempsey-Armidale region of the New England Tableland in northern New South Wales.

The larva has not yet been associated with its adult; however, the relatively small size attained by last instar larvae and somewhat similar distribution patterns suggest that this type may be the larval form of *S. minimus*.

Larvae are similar to larvae of both *S. striatus* and *S. basicollis*

and misidentification can easily occur. However these larvae are generally much smaller in the last instar than those of either *S. striatus* or *S. basicollis*. In addition the central ridge of the ninth tergite of *S.* type C extends completely to the posterior margin which is not the case in *S. basicollis*. This ridge is also much narrower than the equivalent ridge in *S. striatus*.

Sclerocyphon type D

(Figure 3.74, Pls 3.45 - 3.50)

Material Examined

Voucher specimens - QUEENSLAND: (all Lamington National Park), 1 L, 25.*v*.1959, C. Evans, QU; 1 L, May 1959, R. Henzel, QU, 1L, 25.*v*.1959, Coll? QU; 1 L, 6.*xi*.1959, D. Mackenzie, QU.

Description

Last Instar Larva (Figure 3.74, Pls 3.45-3.50)

Total length 7.9 mm, total width 5.4 mm, length of ninth tergite 1.3 mm, width of ninth tergite 1.5 mm.

General shape - Broadly ovate, nearly circular thoraco-abdominal shield. Widest at metanotum/tergite I, decreasing to tergite 9.

Dorsal surface - Medial region brown, lateral laminae yellow. Possibly some bleaching of colour has occurred due to the length of time preserved in alcohol (20 years).

Entire marginal fringe of setae with two bands visible; broad, yellow, regular inner section, and narrow outer section where setae soft, flexible, transparent, tapering to a minute point. Many setae broken off at end of inner section.

Trailing edge of lateral laminae with fringe of fine transparent setae.

Dense, uniform covering of small, dark brown, pointed, cuticular beads over entire surface. Darker, dense clump of beads at junction of body and lateral laminae, beads smaller, sparser on trailing edge of lateral laminae.

Some pores visible between pits on pro-, meso- and metanotum, dense region of pores visible beneath shining mucus on transverse,

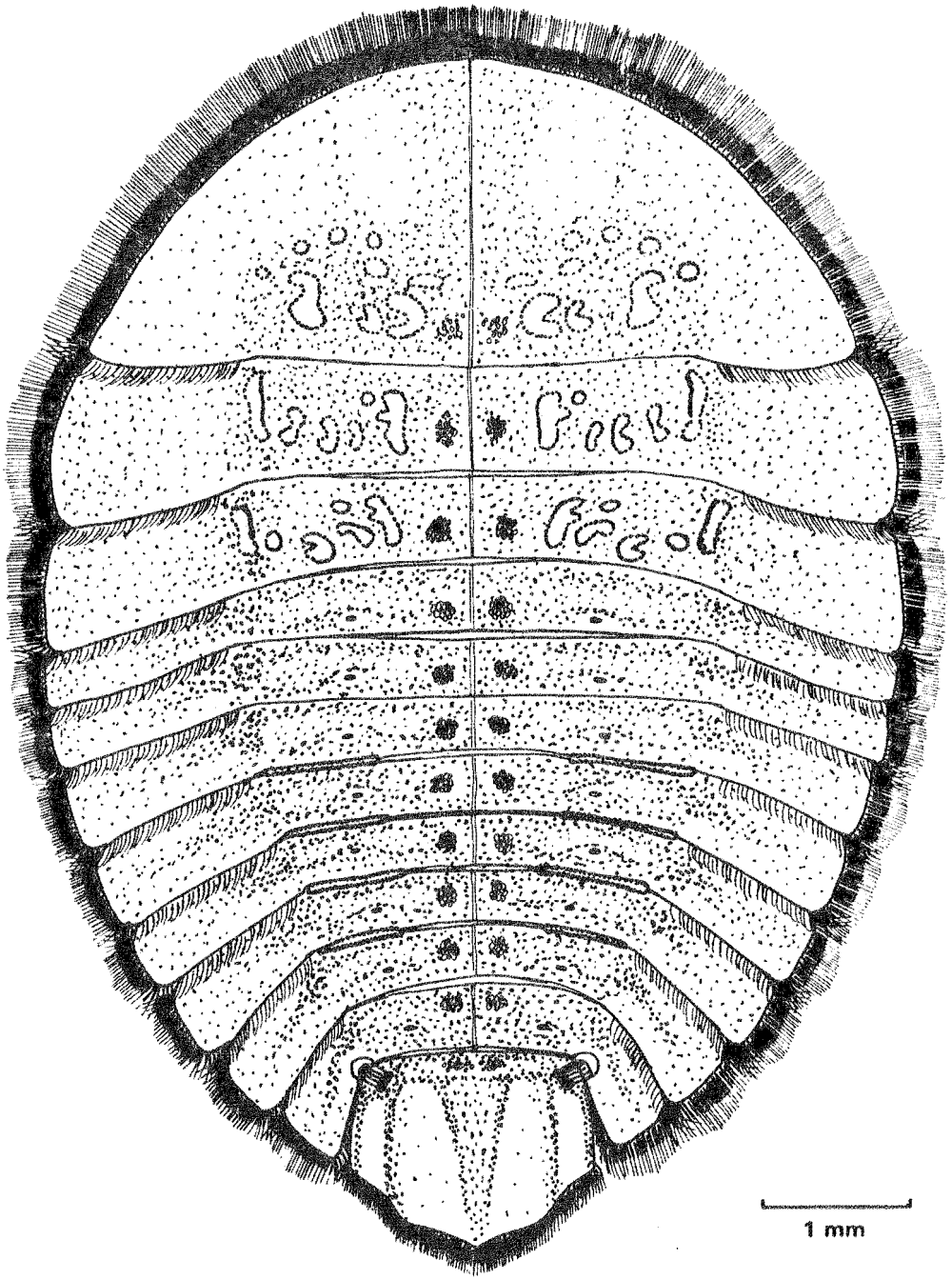
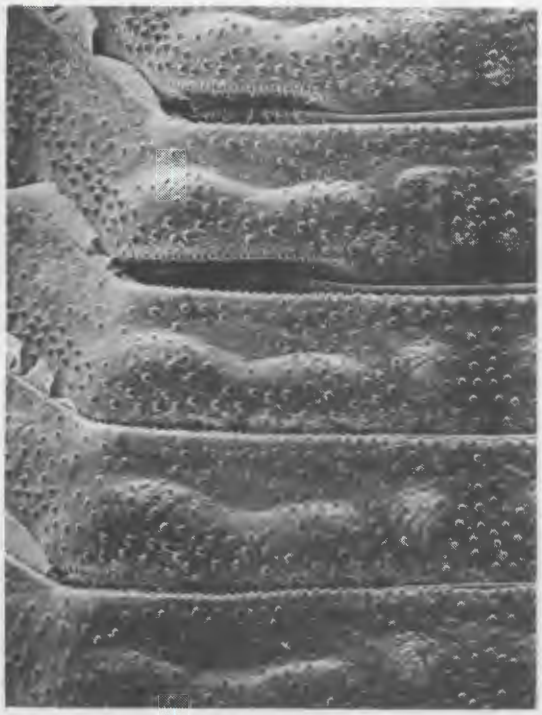
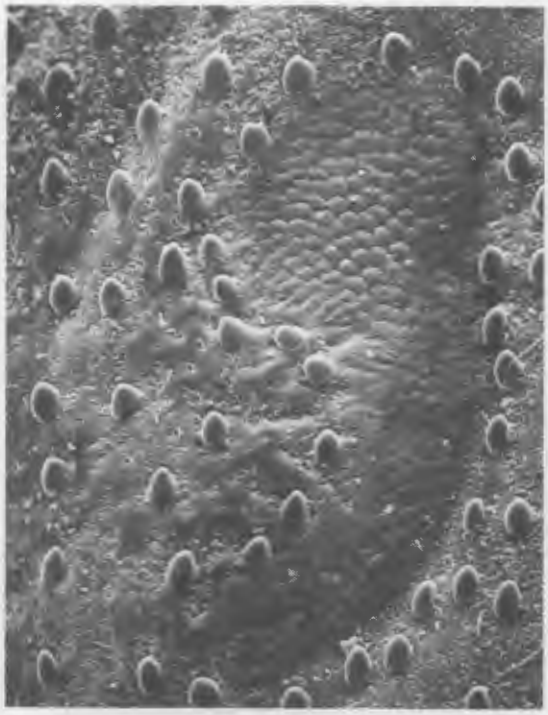


FIGURE 3.74 *Sclerocyphon* type D, last instar larva from Lamington National Park, dorsal view. Scale line = 1 mm.



3.45

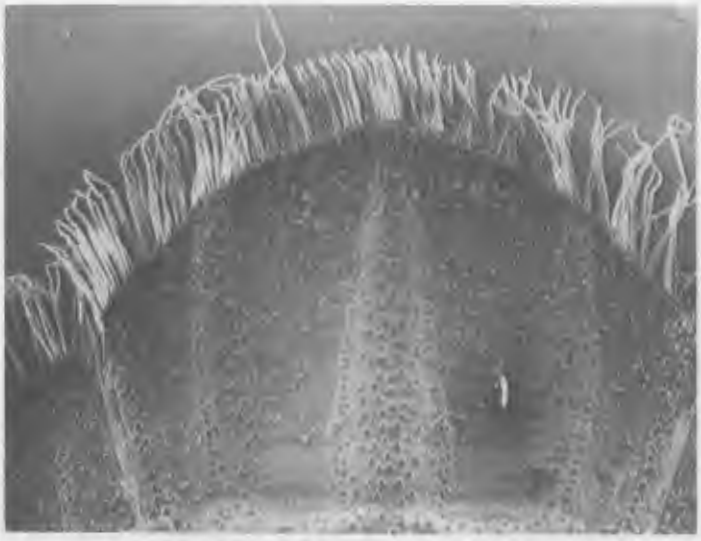
3.46



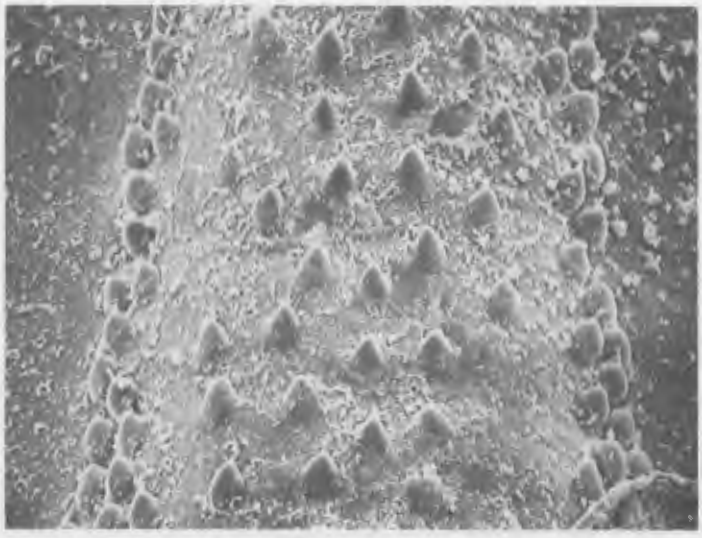
3.47

PLATES 3.45-3.47 *Sclerocyphon* type D, last instar larva from Lamington National Park: (3.45) gin traps, upraised transverse ridges and upraised mid-dorsal regions with clumps of mucous-coated sensilla on tergites 3, 4, 5, 6 and 7, x 40; (3.46) clump of mucous-coated trichoid sensilla , x 400; (3.47) pit on pronotum, x 180.

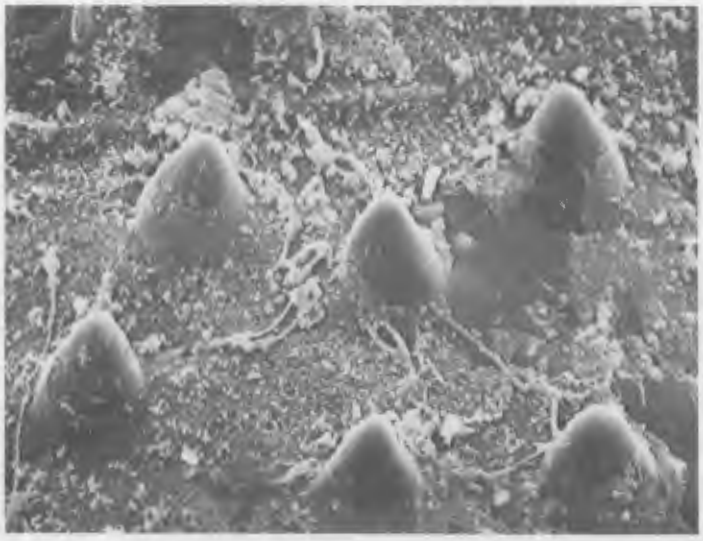
3.48



3.49



3.50



PLATES 3.48-3.50 *Sclerocyphon* type D, last instar larva from Lamington National Park, tergite 9: (3.48) x 40; (3.49) x 200, (3.50) x 650.

upraised strip (Pl. 3.45) above ecdysial scar, each side of midline, on tergites 1-8.

Twelve paired groups of trichoid sensilla in medial region, one group to each side of midline on each thoracic and abdominal segment. Discrete sensilla visible only with scanning electron microscopy (Pl. 3.46). Beneath light microscope each group visible as shining grey circular mucus-coated clumps, some pores visible beneath mucus.

Pronotum with 5 pairs of irregular pits and 4 pairs of circular pits. Meso- and metanotum with 6 pairs of irregular pits. All pits light coloured, bordered by beads (Pl. 3.47).

Four pairs of gin traps present on adjoining margins of tergites 3-4, 4-5, 5-6, 6-7 (Pl. 3.45). Gin traps decreasing in width from anterior pair to posterior pair.

Tergite 9 (Pls. 3.48-3.50) with upraised, tapered central ridge plus a lesser ridge on each side, all extending to posterior margin and outlined with cuticular beads. Two rows of cuticular beads across anterior margin and down each lateral margin. Shining, mucus-coated pored region between two rows of beads at base and down central ridge. Beads smaller, sparser between ridges and posteriorly. Posterior margin pointed at apex, a concave sinuosity present each side of middle, between lateral ridge and lateral margin. Lateral margins short, curved.

Diagnosis

Larvae of this type can be distinguished by the following combination of characters; 4 gin traps, tergite 9 with 3 ridges, each extending to the posterior margin and outlined with cuticular beads, the shining coat of mucus on the anterior margin and the central ridge of tergite 9, and the uniform covering of small, dark cuticular beads over the entire shield.

Comments

Only 5 specimens of this larval type, from one locality, Lamington National Park, have been examined; however, their distinctive morphology warrants recognition as a new larval type. The presence of 4 gin traps clearly separates these larvae from other similar species, including *S. striatus*, *S. basicollis* and *S.* type C, which possess only 3 gin traps.

The larva of this type has not yet been associated with its adult. Possibly it is the larva of *S. nitidus* which also occurs in Lamington National Park. Further collecting and laboratory rearing of the larvae are needed to verify this suggestion.

Sclerocyphon type E

(Figure 3.75)

Material Examined

Voucher specimens - NEW SOUTH WALES: 4 L, Creek E of Nundle, near Tamworth, New England Tableland, 27.*i*.1980, J.A. Smith, NMV; 7 L, same data, held by J.A. Smith.

Other material examined - NEW SOUTH WALES: 1 L, Barrington, 30.*viii*.1931, F.J. Gay, ANIC.

Description

Last Instar Larva (Figure 3.75)

Total length 9.0 mm, total width 4.9 mm, length of ninth tergite 1.2 mm, width of ninth tergite 1.6 mm.

General shape - Elongate-elliptic thoraco-abdominal shield, widest at metanotum, tapering to tergite 9.

Dorsal surface - Medial region dark brown, narrow, yellow longitudinal strip down midline, some yellow patches on tergites. Pronotum with yellow patch above each eye, dark over head. Lateral laminae light brown, yellow patch before edge.

Entire marginal fringe of setae with two bands visible; narrow, light brown, regular, inner section, and wider outer section where setae, soft flexible, transparent, tapering to minute point. Some setae remaining dark for entire length. Trailing edge of lateral laminae with fringe of fine, transparent setae.

Dense, uniform covering of dark brown, sclerotised cuticular beads over entire shield, darker, dense clump of beads at junction of body and lateral laminae of tergites 1-8, beads smaller, sparser at trailing edge of lateral laminae.

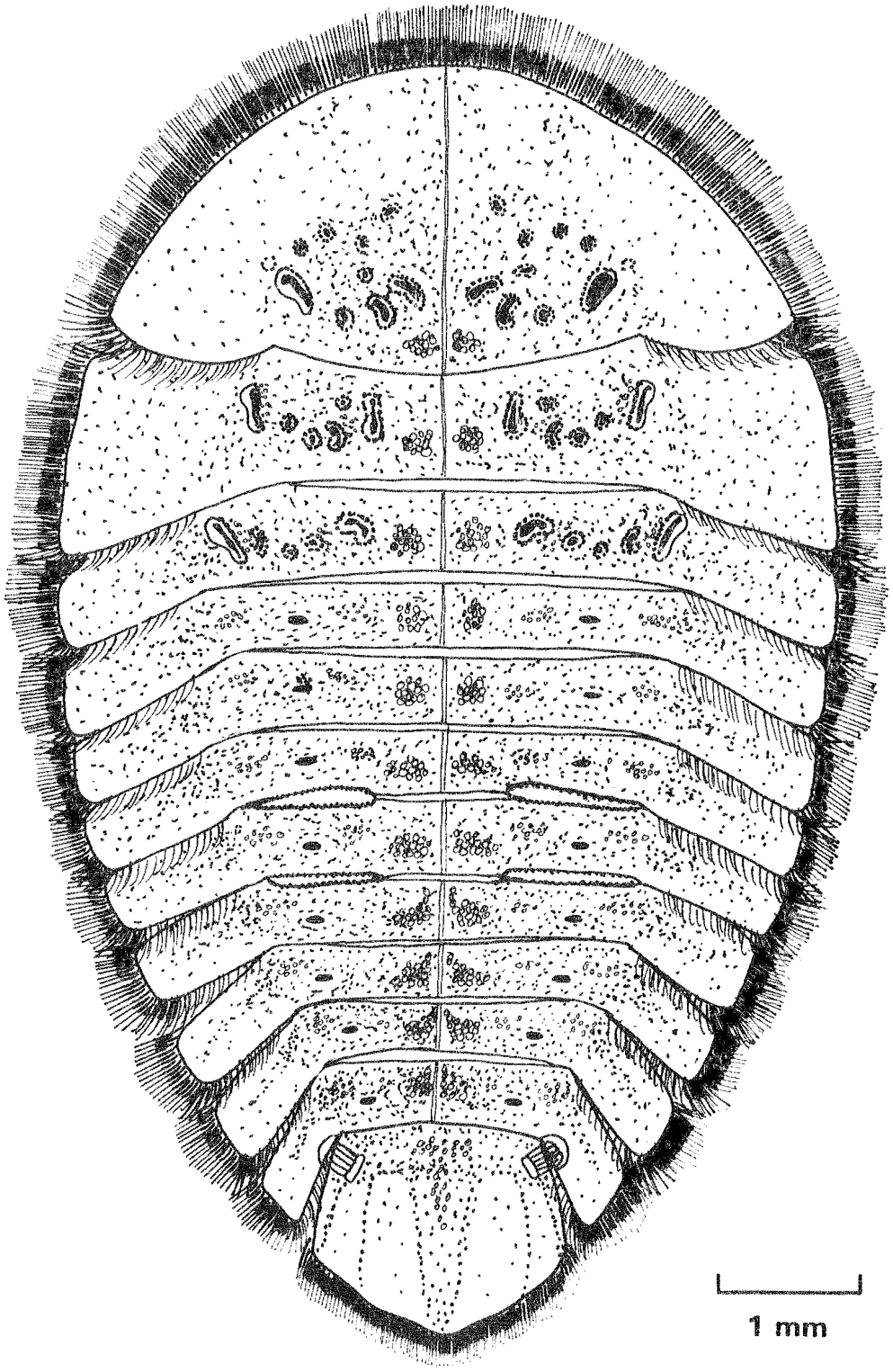


FIGURE 3.75 *Sclerocyphon* type E, last instar larva from creek nr Nundle, dorsal view. Scale line = 1 mm.

Pores scattered over entire shield, densest on slightly upraised transverse strip, above ecdysial scar, each side of midline, on tergites 1-8.

Twelve paired groups of trichoid sensilla in medial region, one group to each side of midline on each thoracic and abdominal segment. Discrete sensilla only visible with scanning electron microscopy. Beneath light microscope each group visible as shining, grey, oval mucus-coated clump, yellow pores visible beneath mucus.

Pronotum with 5 pairs of irregular pits, 4 pairs of circular pits and one anterior pair. Meso- and metanotum with 6 pairs irregular pits. Most pits dark, bordered by cuticular beads.

Two pairs of gin traps on adjoining margins of tergites 3-4, 4-5. Both sets wide, extending nearly to midline.

Tergite 9 with upraised, tapered central ridge extending to posterior margin, a lesser ridge on each side, all outlined by cuticular beads. Beads sparser between ridges and posteriorly. Posterior margin with pointed apex and slight sinuosity each side of middle. Lateral margins fairly straight, sloping outwards.

Diagnosis

The presence of only two pairs of gin traps, on the adjoining margins of tergites 3-4 and 4-5, is a unique character which separates larvae of this type from all other species and larval types of *Sclerocyphon*.

Comments

Only 12 specimens of this larval type, from two localities, both on the New England Tableland, have been examined; however, the possession of only two pairs of gin traps warranted their description as a new larval type. Other features including the form and contouring of the ninth tergite and the form of the mid-dorsal clump of trichoid sensilla

support the recognition of this larval form as a separate type.

This larva has not yet been associated with its adult, several last instar larvae from the creek east of Nundle were held alive in the laboratory but pupation failed to occur.

Sclerocyphon type F

(Figure 3.76)

Material Examined

Voucher specimens - QUEENSLAND: 5 L, Reliance Ck, Mackay, 17.*viii*. 1978, JCUNQ; 2 L, same data, NMV.

Other material examined - QUEENSLAND: 20 L, Amhurst Ck, Mackay, 25.*v*.1978, JCUNQ; 2 L, 36 km S of Miriamvale, 25.*v*.1971, E.F. Riek, PZ; 10 L, Burdekin R., halfway between Townsville and Charters Towers, 10.*viii*.1980, A.J. Dartnall; 2 L, Ugly Gully Ck, Brisbane, date?, PZ; 1 L, Brisbane, 15.*vi*.1955, Kirkpatrick, QU. NEW SOUTH WALES: 1 L, freshwater turtle gut contents, Georges Ck at "Murrungi" on Kempsey-Armidale Rd, 80 km SE Armidale, 25.*xii*.1976, M.K. Notestine; 5 L, tributary of Rocky R, E of Tenterfield, off Bruxner Hwy, 28.*i*.1980, J.A. and J.N. Smith.

Description

Last instar larva (Figure 3.76)

Total length 8.5 mm, total width 4.5 mm, length of ninth tergite 1.7 mm, width of ninth tergite 2.35 mm.

General shape - Elongate-elliptic thoraco-abdominal shield, widest at metranotum, tapering to relatively wide tergite 9.

Dorsal surface - Medial region dark brown, some light patches, narrow yellow longitudinal strip each side of midline, pronotum with large light patch above each eye. Lateral laminae lighter, alternating colour pattern; yellow-brown-yellow-brown. Tergite 9 dark brown with one yellow patch, on each side, below spiracular brush.

Entire marginal fringe of setae with two bands visible; narrow, yellow, regular, inner section, and outer section where setae soft,

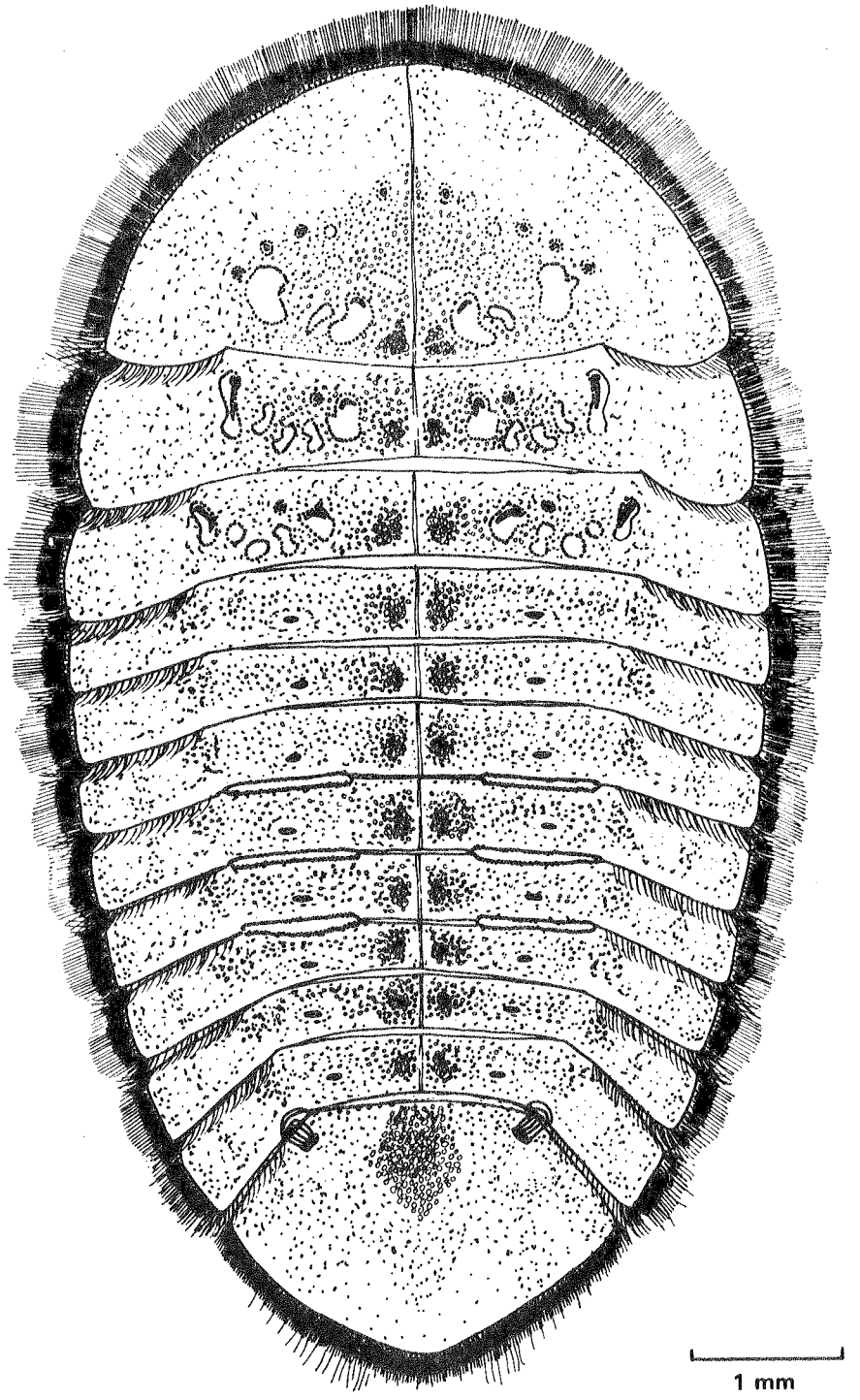


FIGURE 3.76 *Sclerocyphon* type F, last instar larva,Reliance Ck, dorsal view. Scale line = 1 mm.

flexible, transparent, tapering to minute point. Trailing edge of lateral laminae with fringe of fine transparent setae.

Dense covering of dark, sclerotised cuticular beads over entire surface, darker dense clump of beads at junction of body and lateral laminae of tergites 1-8.

Pores visible as shining yellow dots, densest beneath shining yellow coat of mucus between pits on pro-, meso- and metanotum and extending anteriorly along midline on pronotum. Also on two upraised patches, each side of ecdysial scar, each side of midline, on tergites 1-8.

Eleven paired groups of trichoid sensilla in medial region, one group to each side of midline on each thoracic and abdominal segment. Discrete sensilla visible only with scanning electron microscopy. Beneath light microscope each group visible as regular elongate-oval shining, grey, mucus-coated clump, encircled by wide region of pores. Tergite 9 with one large mucus-coated mass medially.

Pronotum with 5 pairs of irregular pits, 4 pairs of regular pits and one anterior pair. Meso- and metanotum with 6 pairs of irregular pits.

Three pairs of gin traps present on adjoining margins of tergites 3-4, 4-5, 5-6. All pairs wide, extending nearly from lamina to mid-point.

Tergite 9 without ridges, broadly triangular, posterior margin widely curved, lateral margins short. Anterior medial region with shining grey mucous mass, devoid of beads, pores visible beneath mucus. Cuticular beads scattered across remainder of tergite 9, largest, densest at anterior and lateral margins, smaller, sparser in posterior region.

Diagnosis

Larvae of this type can be distinguished on the following combination

of characters; 3 pairs of gin traps, broadly triangular ninth tergite lacking ridges, with anterior, medial, grey, mucous mass and shallowly curved posterior margin, and elongate-oval, mucus-coated clumps of trichoid sensilla .

Comments

The distribution of this larval type extends from the Burdekin River in north Queensland to the edges of the New England Tableland in northern New South Wales.

Last instar larvae of this type are usually large in comparison with other larvae from the north of Australia, with the exception of *S.* type A. Larvae are similar, in many aspects, to the larvæ of *S. armstrongi*, however they differ sufficiently to warrant recognition as a new larval type.

3.5 Discussion

Relationships within *Sclerocyphon*

As the adults (and pupae) of *Sclerocyphon* are terrestrial while the larvae are aquatic, relationships within the genus can be most easily recognised by initially treating the different life phases separately.

Adults

The outstanding feature of adult systematics is the morphological similarity of most species with an attendant lack of clear diagnostic characters. This similarity of external characters suggests that common selective pressures are acting on the adults of all species. This could be a result of the following combination of factors: the very short adult life span (restricted to only a few weeks in summer) in comparison to a much longer larval phase (up to 22 months); the cryptic mode of behaviour, exhibited by all beetles, which restricts them to certain microhabitats; and the similarity of habitats (the moss, litter, grass and debris at the edges of rivers and streams).

Early workers, Blackburn (1892), Lea (1895, 1919) and Carter (1935) based specific determinations on differences in size, shape, colour, convexity and pubescence. This study extends that work to include features of the male and female genitalia. The morphological similarity of beetles within many of the dryopoid genera and the need to examine genitalia for specific diagnosis has been commented upon by previous workers. Holland (1972, p.11) notes that in the Helminthidae,

> "on external features alone specific differences within the genera *Oulimnius* and *Riolus/Normandia* are difficult to detect",

and it is often necessary to

> "examine the genitalia before making a positive determination".

Leech and Chandler (1956, p.355) note that for specific determination in the genus *Helichus* (species of which are now included in the same subfamily as *Sclerocyphon*, the Eubriinae)

> "pubescence is the most used character since it covers most of the body, masking many other possible characters. It should always be used with discretion since the specimen may assume quite a different appearance if it is rubbed or soiled with grease or dirt. If one is not familiar with the group it is best to check the male genitalia, especially with ... *(several species)* ... for which no dependable distinguishing characters have been found. Size and slight differences in shape are of limited usefulness and difficult to describe".

Such a comment can be equally applied to *Sclerocyphon*.

In *Sclerocyphon* the ventral surface, as well as the head, antennae and legs, are thickly clothed with dense pubescence and as a result few distinguishing features are visible. While specific differences in the form and density of pubescence on the pronotum and elytra do exist, care must be taken to remember that variation due to abrasion can occur. The shininess of the dorsal surface can also vary, however this character is closely tied with the denseness of pubescence.

Characteristic dorsal and abdominal colour patterns predominate in different species but variability can occur. There is also variability in size. Differences in shape and convexity are evident but as already noted by Leech and Chandler (1956) such features are difficult to describe;

in this work diagrams are used to overcome this problem. The mouth-parts show great uniformity throughout the genus, and as adults do not appear to feed there has probably been little pressure for morphological divergence.

The male genitalia are of the primitive, trilobate form (Britton, 1970), the aedeagus being composed of a single basal piece with a penis, or median lobe, and a pair of parameres, one attached to each side. Boving (1929) considers the Dryopoidea to be derived from byrrhoid ancestors and Crowson (1955) suggests that they have arisen from a line common to both the dascilloids and the byrrhoids. The occurrence of trilobate male genitalia on *Sclerocyphon*, as in the Byrrhoidea, supports these views.

Apart from one striking exception, *S. secretus*, the basic similarity of male and also female genitalia provides much justification for the inclusion of all species within the one genus, *Sclerocyphon*. Specific differences in males are limited primarily to the shape and size of the penile sclerites. Some confusion in identification may still arise both from the subjective nature of these characters and from the genuine similarity of certain species, in particular: *S. aquaticus* and *S. lacustris; S. collaris* and *S. nitidus;* and *S. basicollis* and *S. minimus*. However the form of the female dorso-lateral plates in each species is unique.

The Tasmanian endemic, *S. secretus,* possesses a dorsal penile sclerite armed with two sharp lateral projections or barbs, a feature not present in any other *Sclerocyphon* species. The female possesses dorso-lateral vaginal plates with extended lateral projections that appear to correspond to the barbs of the male. All other aspects of morphology are such that despite the possession of these genital features the placement of this species in a new genus is not warranted.

The evolution of atypical male genitalia may be related to the sympatric occurrence of *S. secretus* and *S. aquaticus* in many Tasmanian

streams, particularly those of the west coast. Although larvae are present throughout the entire year, the period of emergence is restricted to the warmest summer months. Adult activity is also restricted to the warmer daylight hours. The shortness and relative coolness of Tasmanian summers particularly on the west coast suggests that beetles of both species may be forced to emerge simultaneously. Field observations lend support to this view. Adults of both species appear to occupy the same habitats and display similar behaviour. Thus, the unique form of the genitalia of *S. secretus* may well serve to maintain reproductive isolation of the species in localities where adults of both species occur together in time and space. Several Australian mainland species also occur sympatrically (Chapter 4). The variation in form of both male and female genitalia in these cases, while not as striking as that of *S. secretus*, differs sufficiently between species to prevent interbreeding. It is possible that the warmer and longer summers of most Australian mainland localities allows greater temporal separation of adults, resulting in less selection for extreme isolating mechanisms.

Larvae

Like all psephenid larvae, those belonging to the genus *Sclerocyphon* show marked adaptations to life in the lotic environment, the thoracic and abdominal segments forming a dorso-ventrally flattened shield with the head and legs hidden beneath. It is in the features of the dorsal surface of this shield that the greatest variation between species is evident, in contrast to the ventral surface which displays remarkable homogeneity between species. This is probably a consequence of the extreme dorso-ventral flattening as only the dorsal surface is exposed to the external, and more variable, aquatic environment while the ventral surface remains adpressed to the substrate throughout the life of the

larva. This difference in variability between dorsal and ventral surfaces was first noted by West (1929a) in his early comparative work on larval Dryopoidea and it appears that features of the dorsal surface are more significant not only in systematics within the genus but in the higher groupings as well.

In considering larval morphology some deductions concerning phylogeny *sensu* Hennig (1965) can be made. Although it may seem over-meticulous to expend much effort in ascertaining phylogeny within the genus *Sclerocyphon*, the fact that *Sclerocyphon* is the only psephenid genus in Australia and its members inhabit a diverse range of habitats which, on other continents (Africa, Asia and the Americas) are occupied by members of a number of genera of two or more psephenid sub-families, suggests that some discussion of phylogeny within the group is warranted. This interpretation of systematics within *Sclerocyphon* from a phylogenetic viewpoint will also facilitate further work on the phylogeny of the Psephenidae as a whole.

During this attempt to achieve a phylogenetic classification a number of difficulties have become apparent. It is first necessary to establish plesiomorphic (primitive) and apomorphic (derived) character states, as it is the presence of synapomorphy, that is, the common possession of derived characters, that determines the closeness of two species (Hennig, 1965). Unfortunately no fossil *Sclerocyphon* exist and so conclusions as to plesiomorphy and apomorphy must be based entirely on an examination of present day *Sclerocyphon* species and closely related groups. Ross (1967) notes that for Trichoptera much information from outside the families is necessary to establish primitive characters. Such information is also necessary for *Sclerocyphon*, but, as many genera of the Dryopoidea are still little researched, in some cases it is not readily available. Also, psephenid larvae have secondarily invaded the aquatic habitat from land (Hinton, 1955) and in doing so have developed

extreme adaptations to their aquatic environment. Thus, to a certain extent many features of the dorsal shield (and the shield itself) are advanced, making the determination of plesiomorphy and apomorphy one of relativity and hence the more difficult. Furthermore, the very similar features of the ventral surface of species of *Sclerocyphon* probably represent plesiomorphic characters and, as such, contribute little to phylogenetic decisions, as symplesiomorphies cannot be used to establish relationships (Hennig, 1965).

The determination of the Psepheninae as the most primitive psephenid subfamily (Hinton, 1966) does provide some clues as to the possible nature of *Sclerocyphon* ancestors. This study has been facilitated by the provision of specimens of the Psepheninae (in this case, the Canadian water penny, *Psephenus herricki*) by Professor H.B.N. Hynes, for examination and comparison.

Size, Colour and Shape

Size, colour and shape may all vary within some species according to locality. Larval size can vary considerably between different populations of the same species. The variation in colour according to substrate has already been described in Tasmanian species (Smith, 1981) and similar features, particularly the occurrence of disruptive colour patterns in the form of dark and light bands, or patches, are also evident in Australian mainland species.

The variability of shield shape in Tasmanian species has been the subject of a detailed multivariate analysis (Chapter 5). Three species, *Sclerocyphon aquaticus*, *S. zwicki* and *S.* type A exhibit a fairly constant shape, possessing a broadly ovate-circular shield, while other species exhibit a range of forms from the broadly ovate-circular to the narrow-elongate.

The fact that the broad ovate-circular shield appears to be the predominant form in the Psepheninae suggests that this was probably the ancestral psephenid shield form.

Cuticular Beads and Mucus

Inter-specific differences in the shape, density and arrangement of the dark, sclerotised, cuticular beads or granules present on the dorsal surface of the larvae are evident. The shape of beads in each species was best elucidated by scanning electron microscopy as their relatively small size (0.05 mm in height or less) and the buildup of mucus on various parts of the dorsal surface prevented close examination with the light microscope. The functional role of the beads is not entirely clear and is discussed further in Chapter 6. Similar cuticular projections are present in other psephenid genera, although both their structure and arrangement may differ. The relative plesiomorphy or apomorphy of these structures is difficult to determine.

Two species, *S.* type A and *S. zwicki*, differ from all other *Sclerocyphon* in the arrangement of the cuticular beads, as well as several other features. In *S.* type A beads are present, in a very reduced state, on the lateral laminae and entirely absent from the medial region. In *S. zwicki* they are present both laterally and medially but are extremely reduced in the medial region. Both species possess a coating of mucus over the entire medial region, which together with the reduction or absence of beads, results in a smooth, shining appearance. While all other species possess muco-secretory pores over much of the dorsal shield a buildup of mucus usually only occurs in discrete regions. *S.* type A, *S. zwicki* and also *S. aquaticus* larvae possess two longitudinal rows of long black setae each side of the midline, while all other species possess mucus-coated clumps of short sensilla each side of the midline. It is

difficult to comment on the plesiomorphy or apomorphy of these various mucus arrangements. Little mention has been made of the occurrence of such mucus in other psephenid species, however examination of *Psephenus herricki* larvae, in this study, revealed that mucus is present over much of the medial region of the dorsal shield. More information needs to be obtained on the role that mucus plays in the hydrodynamics of larvae. In some circumstances mucus may considerably lessen the drag on a submerged object and thus may be of great advantage to larvae in a particular flow regime (Chapter 6). The different arrangements of mucus on the dorsal surface may represent the most efficient pattern for a particular environment and, as such, be adaptations to specific environmental conditions rather than indicators of evolutionary stages.

Dorsal pits

Depressions or pits, usually bordered by cuticular beads occur on the dorsal surface of all *Sclerocyphon* larvae. The number and arrangement of these is constant within the entire genus. *Sclerocyphon* type A larvae differ from all other species in the possession of extra pits on the abdomen. These longitudinal pits are found at the junction of the body and the lamina, one on each side of the midline, on tergites 1-8.

It is reasonable to assume that the pits play a sensory role as they are situated on the dorsal surface and occur in greatest density on the thorax, which is the highest region of the larva projecting into the external flow and thus the first region in contact with the external flow, at least, when the larva is orientated in the direction of flow. While this character constitutes little to the understanding of systematics within *Sclerocyphon*, the occurrence of similar pits in both other eubriine genera and also the Psepheninae (although arrangement and number may differ) represents the common possession of a derived character, that is, synapomorphy. This supports Hinton's (1955, 1966) proposed monophyly

of the two subfamilies. Similarly, the marginal fringe of *Sclerocyphon* varies little within the genus, but its similarity to that of *Psephenus herricki* is such as to suggest synapomorphy, rather than convergence, between the two subfamilies.

Gin traps

Sclerocyphon species can be arranged in three groups according to the presence of two, three of four pairs of gin traps on the abdominal tergites. The species that occur within each group are listed in Table 3.1. The term "gin trap", as applied to the Coleoptera, was first used by Hinton (1946). He noted that pupae of a number of unrelated beetles had the adjacent margins of one or more pairs of abdominal segments sclerotised, forming a simple mechanism for pinching attacking insects. Median dorsal gin traps occur in the pupae of the Dermestidae, Scarabeidae, Cerambycidae, Coccinellidae, Ptilodactylidae, Dryopidae and Psephenidae while lateral gin traps occur in the pupae of the Tenebrionidae and Colydiidae. The occurrence of gin traps in larvae appears to be restricted solely to *Sclerocyphon*.

The gin traps of *Sclerocyphon* larvae and pupae are constructed in a similar manner to those of the pupae, described by Hinton (1946). Each gin trap consists of two strongly sclerotised, beaded, or toothed, ridges separated by a deep depression. When the larva is relaxed the abdominal tergites are separate and the jaws of each gin trap are held open, when the larva is touched the abdomen contracts, the tergites close up, and the jaws of each gin trap meet. Hinton (1946) concluded that gin traps are organs of defence after conducting a number of simple experiments, with *Dermestes* pupae, in which the gin traps were observed to close on the legs of invading mites.

In those species of *Sclerocyphon* in which the pupae were available for examination (seven) the gin trap number was found to be the same in both the larva and the pupa, except for two species; *S. aquaticus*

TABLE 3.1 Species-groups in *Sclerocyphon* based on differences in larval gin trap number.

Locality	A 4 pairs of gin traps	B 3 pairs of gin traps	C 2 pairs of gin traps
Australian mainland	*S. maculatus*	*S. striatus*	*S.* type E
	S. type A	*S. basicollis*	
	S. type D	*S. armstrongi*	
		S. zwicki	
		S. type B	
		S. type C	
		S. type F	
Tasmania	*S. aquaticus*		
	S. secretus		
	S. lacustris		

and *S. maculatus*.

In these two species larval gin trap number is four while pupal gin trap number is five, a fifth somewhat reduced pair being present on tergites 7 and 8. This suggests that at an earlier time gin traps were present on more abdominal tergites. Therefore it appears that the observed reduction in gin trap number within the species of *Sclerocyphon* represents degrees of apomorphy.

Bertrand and Watts (1965) described an apparent reduction in gin trap number from four pairs in the last instar larva to three in the earlier instars in two Tasmanian species of *Sclerocyphon*, *S.* sp.5 and an undescribed species. However, this feature has not been observed in any larvae examined in the present study, the gin trap number appears to be constant, for all instars, within any particular species.

In all species, the gin traps are present on the same tergites, the most anterior pair occurring on tergites 3 and 4. Within a species the gin traps are always of equal length, except in those species possessing four, in which the posterior pairs (on tergites 6 and 7) are always much narrower, often less than half the width of preceding pairs. The reduction of this posterior pair may well be a step towards complete loss, which would then place them within the three gin trap group.

The actual process of reduction in gin trap number appears to be occurring in *S. zwicki*. Three pairs of gin traps are normally present but several larvae examined possessed two narrow bands of sclerotisation on the posterior margin of tergite 6, where the anterior ridges of a fourth pair would be expected to occur, that is, the larvae possess "three and a half" pairs of gin traps. *S. maculatus* is somewhat aberrant, in all four pairs of gin traps only the lower margins are heavily sclerotised, giving the effect of four "half" gin traps. In this species it appears that all pairs of gin traps are undergoing reduction simultaneously.

Hinton (1946) discussing the phylogeny of the Dermestidae, suggests that in this family,

> "as new habits and structures which serve to protect the pupa are acquired the number of dorsal gin traps is reduced".

This may also be the case in *Sclerocyphon*. While the gin traps probably do serve as defensive structures the extremely hard cuticle of the dorsal surface reinforced with the sclerotised cuticular beads probably provides considerable protection against attack by arthropod predators such as odonatan and plecopteran nymphs and trichopteran larvae.

The reduction of gin traps from four to three always involves the loss of the traps on the posterior segments. It is on these segments that the gin traps are probably least efficient, as the angle of incline of the abdomen is considerably lower in this region and provides less mechanical advantage to the gin traps.

Bertrand and Watts (1965) noted the presence of gin traps in *Sclerocyphon* larvae but attached little taxonomic significance to them, probably because of the limited range of material that was available to them. However, Bertrand (1969) includes gin trap number in his specific diagnoses.

Morphology of Tergite 9

Three species-groups, somewhat different to those based on gin trap number can be formed on the basis of tergite 9 morphology. These species-groups are listed in Table 3.2 (columns I, II and III) and the form of the ninth tergite in each species is illustrated in Figure 3.9.

The first grouping (column I) is composed of larvae in which tergite 9 is square or rectangular in outline with the posterior margin produced

TABLE 3.2 Species-groups in *Sclerocyphon* based on differences in the morphology of larval tergite 9.

Locality	I Tergite 9 square-rectangular, posterior margin regularly curved, longitudinal ridges present (except *S.* type A)	II Tergite 9 approximately triangular, posterior margin sinuous, longitudinal ridges absent.	III Tergite 9 approximately semi-circular, posterior margin sinuous, longitudinal ridges present.
Australian mainland	*S.* type A (not ridged) *S. zwicki*	*S. maculatus* *S. armstrongi* *S.* type F.	*S. striatus* *S. basicollis* *S.* type B *S.* type C *S.* type D *S.* type E
Tasmania	*S. aquaticus*		*S. secretus* *S. lacustris*

in a regular curve. This grouping is somewhat diverse. *S.* type A is the most extreme form possessing a ninth tergite that is completely flat, *S. zwicki* and *S. aquaticus* both display longitudinal ridges. *S. aquaticus* also possesses slight sinuosities on the posterior margin, a character more associated with the *S. striatus* species-group (column III).

The second grouping (column II) is that in which tergite 9 is triangular in outline, sinuous but lacking distinct longitudinal ridges, although the mid region is raised rather than flat. This group is best characterised by *S. maculatus*.

The third grouping (column III) represents the most common form of tergite 9, in which the tergite is approximately semi-circular but either lightly or heavily sinuous and with three longitudinal ridges, either weakly or strongly upraised. This group is characterised by *S. striatus* (possibly the most common Australian species) which possesses well defined sinuosities and three strongly upraised ridges.

The ninth tergite is periodically raised in the vertical plane, by the larva, to enable active ventilation of the extruded tracheal gills beneath. The shape and contouring of this segment is thus very important to the hydrodynamics of the larva. This aspect is discussed further in Chapter 6. In considering larval hydrodynamics it is reasonable to suggest that *S. striatus*, with its strongly upraised ridges and deep sinuosities serving to channel fluid flow across the tergite, possesses the most advanced tergite 9 form. Conversely *S.* type A with its virtually square ninth tergite, lacking ridges or sinuosities, probably represents the most primitive form. The triangular form of tergite 9 found in *S. maculatus* lacks discrete ridges but by virtue of its shape would still effect control on the fluid passing over it. It is difficult to say how efficient this control may be in comparison to that of the *S. striatus* species-group.

Tergite 9 morphology varies little within the Psepheninae and

Eubrianacinae and the ninth tergite in these two groups is much smaller than that of the Eubriinae. However the former two subfamilies possess ventral abdominal gills rather than extrusible anal gills and thus there is no need for the marked vertical elevation of tergite 9 that is required by the Eubriinae for gill ventilation. The ninth tergite of *Psephenus herricki* is nearly square with a regularly curved posterior margin and no ridges (Chapter 6) and thus most closely resembles the ninth tergite of *S.* type A. This possibly provides further evidence for the claim already made that *S.* type A tergite 9 morphology is the plesiomorphic expression of tergite 9 form within *Sclerocyphon*.

The shape of the ninth tergite varies considerably amongst the Eubriine genera. However the presence of longitudinal ridges appears to be confined to *Sclerocyphon* and a group of Chilean larvae designated *Tychepsephenus* by Artigas (1963) but which should most probably be included in *Sclerocyphon* (discussed further in the following section). Bertrand (1972) uses the shape of tergite 9 as a diagnostic character at the generic level, describing tergite 9 of *Sclerocyphon* as *"plus ou moins subtriangular"*. As this character has now been shown to vary between species within *Sclerocyphon*, Bertrand's (1972) key can no longer be considered valid in its application to *Sclerocyphon*. Previously, Bertrand and Watts (1965) have considered the shape and contouring of tergite 9 to be of primary diagnostic importance in *Sclerocyphon* although they did not speculate on the phylogenetic significance of this character.

The species-groups based on tergite 9 morphology differ somewhat in composition from the groups based on gin trap number, indicating that the two character sets are evolving at different rates. The former groups, rather than the latter, appear to be the more natural groupings as species within those groups, in particular those of column III, are

related on the basis of a number of other features as well. Table 3.2 has been separated into two sections, Australian mainland species and Tasmanian species, to further delineate natural groupings. The Tasmanian species appear to be more closely related to each other, on a number of features including; the gin trap number, the form and distribution of the cuticular beads, and the pattern of distribution of mucus on the dorsal surface, than to any Australian mainland species.

Taxonomic Conclusions

Table 3.3 presents a summary of the chief diagnostic larval characters used to distinguish *Sclerocyphon* species. The presumed plesiomorphic/apomorphic condition of characters (where determined) is also indicated. A phylogenetic tree (Figure 3.77) has been drawn from the information presented in Table 3.3. This diagram represents one possible interpretation of the available data but many more are possible. Platnick (1977) demonstrates that four possible cladograms and 22 possible phylogenetic trees can be drawn up for the same three taxa. The cladograms represent degrees of relationship (i.e. closest relatives) while phylogenetic trees illustrate ancestor-descendant relationships. The number of different phylogenetic trees that can be drawn up for the 14 species (and larval types) of *Sclerocyphon* is thus considerable even taking into account the available evidence concerning the plesiomorphy and apomorphy of various characters. Mayr (1969) notes that the phylogeny illustrated in a phylogram (phylogenetic tree) is inferred rather than real and thus can only be an approximate representation. He also states that it is virtually impossible to represent phylogeny adequately in a diagram due to the fact that different characters evolve at different rates, that is, the occurrence of "mosaic evolution". This has already been demonstrated for two characters; gin trap number and tergite 9 morphology, in *Sclerocyphon*. Thus it would be unrealistic to suggest that Figure 3.77 is an exact representation of phylogeny within

TABLE 3.3 Diagnostic larval characters in *Sclerocyphon*

	Characters	Species													
		S. type A	*S. zwicki*	*S. aquaticus*	*S. secretus*	*S. lacustris*	*S. maculatus*	*S. armstrongi*	*S.* type F	*S. striatus*	*S. basicollis*	*S.* type B	*S.* type C	*S.* type D	*S.* type E
*P	Tergite 9 square-rectangular, posterior margin regularly curved	X	X	X											
*A	Tergite 9 triangular, posterior margin sinuous						X	X	X						
A	Tergite 9 semi-circular, posterior margin sinuous				X	X				X	X	X	X	X	X
P	Tergite 9 without ridges	X					X	X	X						
A	Tergite 9 with ridges weakly upraised					X					X	X			
A	Tergite 9 with ridges strongly upraised		X	X	X					X			X	X	X
P	4 pairs of gin traps	X		X	X	X	X								
A	3 pairs of gin traps		X					X	X	X	X	X	X	X	
A	2 pairs of gin traps														X
	2 longitudinal rows of black setae mid-dorsally	X	X	X											
	Mid-dorsal sensilla in elongate-oval mucus-coated clumps				X			X							
	Mid-dorsal sensilla in circular mucus-coated clumps								X	X				X	X
	Mid-dorsal sensilla in shining inverted "Y"-shaped mucus-coated clumps						X								
	Mid-dorsal sensilla in circular mucus-coated clump outlined by ring of shining yellow pores									X					
	Mid-dorsal sensilla visible as discrete mucus-coated structures not clumps					X									
	Mid-dorsal sensilla with ornately sculptured mucus-coat visible beneath SEM.											X			
P	Constant ovate-circular shield shape	X	X	X											
A	Variable shield shape				X	X	X	X	X	X	X	X	X	X	X
	Entire dorsal medial region with thin coat of mucus	X	X												
	Dorsal-medial region with strip of mucus above ecdysial scar, each side of midline			X	X	X	X	X				X	X	X	X
	Dorsal-medial region with 2 discrete clumps of mucus, one each side of midline								X	X	X				
	Cuticular beads minute, absent or very reduced in medial region	X	X												
	Cuticular beads clearly visible on body and laminae			X	X	X	X	X	X	X	X	X	X	X	X
	Irregular fringe of dark brown setae overlying regular marginal fringe	X	X	X											
	Regular marginal fringe only				X	X	X	X	X	X	X	X	X	X	X

* P = Plesiomorphic character

* A = Apormorphic character

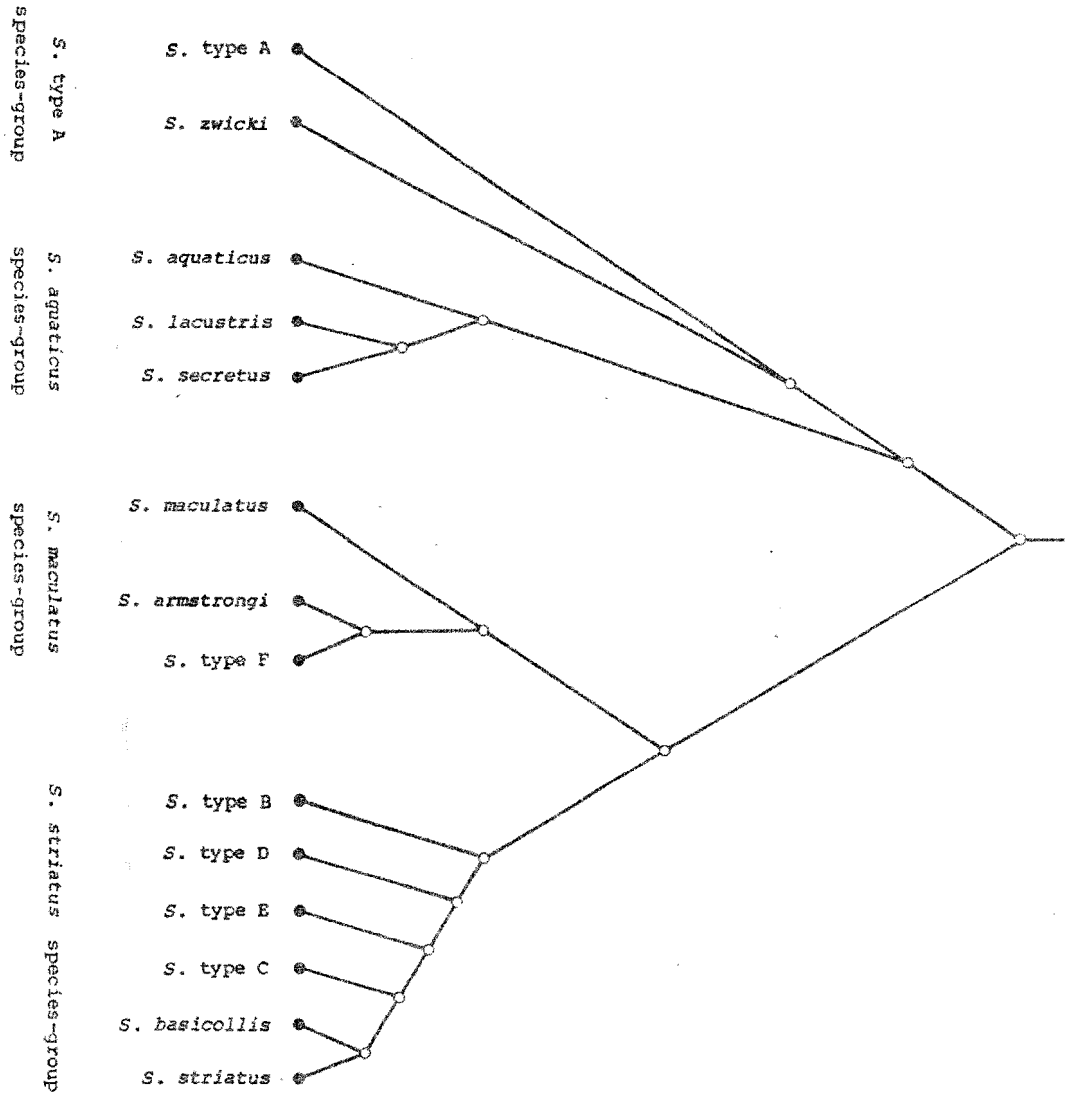


FIGURE 3.77 Phylogenetic tree showing relationships within *Sclerocyphon* based on larval characters.

Sclerocyphon; it does, however, provide some basis for discussion.

Three species, *S.* type A, *S. zwicki* and *S. aquaticus* (all in column I, Table 3.2) appear, on a number of features, to be the most primitive *Sclerocyphon* species. The occurrence of symplesiomorphy however cannot be regarded as evidence of close relationship (Hennig, 1965) and, as indicated in Figure 3.77, it is likely that the three species separated at a very early period in their evolutionary history. However from these three species a certain amount of information on the ancestral form of *Sclerocyphon* can be inferred. All three species (on present information) inhabit permanent rivers and streams of moderate to fast, constant flow regime and it is likely that this represents the habitat first occupied by *Sclerocyphon* larvae. Such habitats would have been most common in Australia during the Tertiary but considerably more restricted during the Pleistocene, an epoch of profound climatic changes (Chapter 4). This decrease in constant flow regime habitats and increased competition would have necessitated the invasion of more variable habitats (in the extreme case those streams that dry up into pools in summer yet also suffer severe spates in winter). Accordingly, larvae developed features that would enhance their survival in such habitats. The species that are capable of living in such habitats appear to be more common and widespread and thus can be considered more successful now than those restricted to the rivers and streams of constant flow regime and constant temperature. This is demonstrated by three species within the *S. striatus* species-group (column III, Table 3.2), which probably represents the most advanced group. Between them, *S. striatus, S. basicollis* and *S.* type C are the most common and the most widespread of all the species of *Sclerocyphon* (Chapter 4). In contrast *S. zwicki* and *S.* type A are more restricted in distribution and where they occur sympatrically with species of the *S. striatus* group often occur in lower numbers.

S. type A is apparently a relict species being known only from the Atherton Tableland region of north Queensland (Chapter 4). Its possession of several unique larval features indicates that the creation of a new genus, representing a more primitive taxon than *Sclerocyphon*, may be warranted. However its similarity, on other characters, to *S. zwicki* which in turn shares a number of common features with all other *Sclerocyphon* species justifies its retention within the genus at this stage. The linking of *S.* type A with its adult will help clarify this situation.

In reconstructing the evolutionary history of *Sclerocyphon* it is somewhat difficult to decide where the *S. maculatus* species-group is best placed. *S. maculatus* differs from all other species in the possession of uniquely shaped, upraised, mid-dorsal clumps of sensillae which are thickly coated with mucus. Its presence in large numbers in many Victorian streams (Chapter 4) indicates that it is a successful species, however the presence of certain plesiomorphic features (four pairs of gin traps and lack of ridges on tergite 9) suggests that it is less advanced than species of the *S. striatus* group. *S. armstrongi* and *S.* type F more closely resemble each other than *S. maculatus* and while grouped with *S. maculatus* on the basis of tergite 9 morphology, in several other features they resemble species of the *S. striatus* grouping.

It has already been suggested that the *S. striatus* species-group represents the most advanced *Sclerocyphon* larval form. The occurrence of a number of synapomorphies between *S. striatus*, *S. basicollis* and *S.* type C indicates only recent splits between these species. *S. striatus* and *S. basicollis* are the most closely related differing only in the form of tergite 9. *S. striatus* displays the more advanced form and thus *S. basicollis* probably more closely resembles the parent species. Although *S.* type D resembles *S. striatus* on tergite 9 morphology,

in several other features it resembles species of the *S. striatus* grouping.

It has already been suggested that the *S. striatus* species-group represents the most advanced *Sclerocyphon* larval form. The occurrence of a number of synapomorphies between *S. striatus*, *S. basicollis* and *S.* type C indicates only recent splits between these species. *S. striatus* and *S. basicollis* are the most closely related differing only in the form of tergite 9. *S. striatus* displays the more advanced form and thus *S. basicollis* probably more closely resembles the parent species. Although *S.* type D resembles *S. striatus* on tergite 9 morphology, its possession of four gin traps sets it slightly apart from all other species in the group although this is possibly only a reflection of different evolutionary rates in these two characters. Similarly *S.* type E, which possesses only two pairs of gin traps, could be separated from the other species of its group on this character. *S.* type B, to a certain extent, represents an intermediate form between the *S. striatus* and *S. maculatus* species-group, possessing a ninth tergite that is more triangular than semi-circular in outline. However, the possession of longitudinal ridges places it within the *S. striatus* species-group.

The three Tasmanian species, *S. aquaticus*, *S. secretus* and *S. lacustris* form a separate species-group. It has already been noted that they appear to be more closely related to each other than to any Australian mainland species. They have probably all evolved from a single ancestral species that also existed on the Australian mainland at some stage prior to the first flooding of Bass Strait (Chapter 4). From this ancestral species two daughter species evolved, probably after the land link between Tasmania and the Australian mainland was severed. One daughter species is represented, now, by *S. aquaticus* while the second daughter species underwent a further split resulting in the formation of two sister species now represented by *S. secretus* and *S. lacustris*. This proposed

phylogeny is based on the fact that *S. aquaticus* possesses more primitive features than *S. secretus* or *S. lacustris* which in turn share many synapomorphies.

S. secretus appears to be the most advanced and successful Tasmanian species, being the most widespread and abundant (Chapter 4) and occupying a diverse range of habitats. In both morphology and habitat range *S. secretus* most closely resembles *S. striatus* on the Australian mainland while *S. aquaticus* is analogous to *S. zwicki*.

S. lacustris has probably evolved in response to an extremely specialised niche in the lacustrine habitat, being restricted solely to the rocky shores of the lakes of the Central Plateau of Tasmania. An analogous lacustrine species has not been found on the Australian mainland. However, rocky lacustrine habitats suitable for supporting larval populations of *Sclerocyphon* are considerably more common in the Central Plateau of Tasmania than in any region of the Australian mainland.

Overall, speciation in the Tasmanian species of *Sclerocyphon* appears to parallel that of the species of Australian mainland *Sclerocyphon*. That is, the evolutionary progression of species from a single ancestral form restricted to fairly constant lotic habitats to more advanced forms inhabiting diverse and variable hatitats has occurred separately, but in a similar fashion, in both Tasmania and on the Australian mainland. The occurrence of a plesiomorphic feature, four pairs of gin traps, in all Tasmanian species suggests that the evolution of this character, at least, is proceeding at a slower rate than in many of the Australian mainland species.

The above argument implies the presence of a common ancestral species of *Sclerocyphon* in both Tasmania and on the Australian mainland prior to the Pleistocene and no re-invasion from the Australian mainland during the Pleistocene. The validity of this point is discussed further in

Chapter 4.

In conclusion it must be noted that although this interpretation of the phylogenetic history of *Sclerocyphon* has been based only on the larval stage it may still be considered valid according to Hennig (1965), who states that it does not matter

> "which stage of development is used to establish relationship on the ground of synapomorphy"

and that

> "a monophyletic group remains such even if it can be established only with the characters of a single stage of development".

One important feature of the adults does contribute to the proposed phylogeny, that is, the striking morphological similarity of all adults provides much evidence for the inclusion of all species (for which adults have been described) within one group, *Sclerocyphon*.

Comparison of the Present Study with Previous Work on Larval *Sclerocyphon*

It has already been noted (Chapter 2) that previous work on *Sclerocyphon* larval systematics is confined to two studies, those of Bertrand and Watts (1965) and Bertrand (1969). Probable identifications of the five larval types described by Bertrand and Watts (1965) and the eight larval types described by Bertrand (1969) are listed in Table 3.4 and Table 3.5, respectively.

Bertrand and Watts (1965) describe the larva and pupa of a species designated "*Sclerocyphon fuscus* Armstrong *in litteris*". This name however is a *nomen nudum* as no description of the adult has ever been published. The species is described for the first time in the present study, (on the basis of adult and larval material) as *Sclerocyphon armstrongi*. They suggest that the larva designated as *S.* sp.5 may be the

TABLE 3.4 Probable identifications of Bertrand and Watts' (1965) larval types.

Sclerocyphon larval types described by Bertrand and Watts (1965)	Probable identifications (present study)
S. sp. 1	*S. striatus*
S. sp. 2	*S.* type C
S. sp. 3	*S. maculatus*
S. sp. 4	*S. armstrongi*
S. sp. 5	*S. secretus*

TABLE 3.5 Probable identifications of Bertrand's (1969) larval types.

Sclerocyphon larval types described by Bertrand (1969)	Probable identifications (present study)
* *S.* sp. A	** *S.* type F
S. sp. B	*S.* type C
* *S.* sp. C	** *S. basicollis*
* *S.* sp. D	** *S. basicollis*
* *S.* sp. E	** *S.* type C
S. sp. F	*S. maculatus*
S. sp. G	*S. zwicki*
* *S.* sp. H	** *S. striatus*

Description of these species* is based on early instar larvae, i.e. not last instar larvae (Bertrand, 1969). It is only possible to make positive identifications on last instar larvae thus the identifications given here** must be regarded as tentative.

larva of *S. aquaticus* by virtue of its occurrence in localities from which adults of *S. aquaticus* have also been recorded. *S.* sp.5 is in fact synonymous with *S. secretus*, the adults and larvae of *S. aquaticus* and *S. secretus* respectively have been linked, in the present study, by laboratory rearing.

One species, *S.* sp.3, now identified as *S. maculatus*, is recorded from Deloraine, Tasmania, representing the only record of this Victorian species in Tasmania. No other Australian mainland *Sclerocyphon* species have been recorded from Tasmania. Dr. Watts kindly made the specimens on which their study was based available to me for examination and I was able to confirm the identification of the two *S.* sp.3 larvae as *S. maculatus*. However, despite intensive collection in the Deloraine area, no specimens of this species were obtained in the present study. Until further specimens of *S. maculatus* can be found in the region, or anywhere else in Tasmania, some doubt as to the validity of the given locality must exist.

Bertrand (1969) uses not only the form and contouring of tergite 9 for specific diagnosis but also the presence of long setae on the posterior margin of tergite 9 and the colouration of this tergite. Neither of the two latter characters are considered valid in the present study, since long setae have been observed on the posterior margin of tergite 9 in all species examined while colour patterns appear to be highly variable within a single species.

Bertrand and Watts (1965) establish specific characters for species on features of last instar larvae only. Hinton (1955) first noted that last instar larvae are easily recognised by the presence of a pair of spiracles on tergite 8 and corresponding spiracular brushes on tergite 9. Similarly only features of last instar larvae have been used for species diagnosis in the present study. However Bertrand (1969) has described five of his eight larval types on larvae of instars earlier than the last.

This has created inaccuracies and several of his larval types appear to represent the same species.

The Relationship of *Sclerocyphon* to Other Eubriine Genera

As noted previously, in his early comparative work on the Dryopidae (= Dryopoidea), encompassing the Psepheninae (= Psephenidae), Dryopinae (= Dryopidae) and Elmidae (= Helminthidae), West (1929a), observed that it was features of the dorsal surface or "those portions of the anatomy most freely exposed, and hence liable to be affected by environmental conditions" that differed between the species he was studying. On the other hand he demonstrated that features of the ventral surface, such as mouth parts and legs, exhibited remarkable constancy. In accordance with these early observations, *Sclerocyphon* shows much similarity to all other psephenid larvae in features of the ventral surface (with the exception of the gills), and it is in features of the dorsal surface that the greatest differences are evident.

Both Bertrand (1972) and Brown (1976) give generic keys based on features of the dorsal surface, in particular, on the tergites 8 and 9. Each eubriine genus displays differences in the development of lateral projections on tergite 8 (and often in the lateral projections of all tergites), the position of spiracles on tergite 8 and the morphology of tergite 9. In addition, *Sclerocyphon* can be immediately separated from all other Eubriinae by the presence of gin traps and the possession of only two anal tracheal gill tufts. All other eubriine genera, and all the Psephenoidinae, possess anal tracheal gills which are divided into three discrete tufts. It is in the possession of only two anal tracheal gill tufts, rather than three, that *Sclerocyphon* may be regarded as the most primitive genus of the Eubriinae. The occurrence of three gill tufts appears to represent an increase in the

respiratory surface area (in comparison to that available with two gill tufts) and so represents the more advanced, or apomorphic, form of gill structure. However measurements of both the surface areas of the two-tufted gills of *Sclerocyphon* and the three-tufted gills of other eubriine genera must be made before this hypothesis can be validated.

In *Sclerocyphon* the shape of the thoraco-abdominal shield varies both within species (probably in response to certain environmental factors, Chapter 5) and between species. The genus therefore encompasses a range of forms displayed by other eubriine genera, from the broadly ovate-circular shields similar to *Afroeubria* (and also the larvae of Psepheninae and Eubrianacinae) to the narrow elongate shields similar to *Eubria* and *Acneus*. In most eubriine genera the thoracic and abdominal tergites (except the ninth) are extended laterally as narrow elongate projections, often recurved and widely separate from each other. However, in *Sclerocyphon* and also the African *Afroeubria* and the Central American *Pelonomus*, the tergites project laterally as wide flattened laminae, each one in close contact with the laminae of adjacent tergites. In *Sclerocyphon* the laminae of tergite 8 also project posteriorly in close opposition to tergite 9. On the former feature *Sclerocyphon* bears a closer resemblance to the larvae of the Psepheninae and Eubrianacinae, and on the latter, the Eubrianacinae, than it does to most other Eubriinae.

Sclerocyphon, therefore, is quite distinct from all other known Eubriinae. A notable exception is a larval form from Chile, designated *Tychepseph⌣us* (?) by Artigas (1963). From his drawings and description these larvae appear to so closely resemble *Sclerocyphon* that their inclusion within the genus must be considered. Not only the mouth parts and legs (which are similar throughout the family) but also the thoraco-abdominal shield with wide, flattened laminae, the

dense covering of cuticular beads, the marginal fringe, the presence of a pair of spiracles at the junction of the body and laminae on tergite 8, the close opposition of the laminae of tergite 8 to tergite 9 and the shape and contouring of tergite 9, are all identical to those of *Sclerocyphon*. On the basis of tergite 9 morphology the larvae appear closest to *S. zwicki* and *S. aquaticus*. Unfortunately Artigas (1963) does not make any mention of the presence of gin traps nor the form of the anal tracheal gills (which in his Figure 10 are obviously retracted beneath the operculum and the ninth sternite). A knowledge of both these structures is necessary for the positive inclusion of the Chilean larvae within *Sclerocyphon*.

The larvae are not definitely associated with an adult form, however Artigas (1963) suggests that they may be the larvae of *Tychepseph͡us felix* Waterhouse by virtue of the fact that it is the only psephenid species recorded from Chile. *T. felix* was described in 1876 from the central region of Chile (Waterhouse, 1876), being a new genus and species within the Psepheninae. However, Artigas's (1963) larvae obviously belong to the Eubriinae (on the features described above). Association of these larvae with their adult is needed before a positive identification can be made.

Although *Sclerocyphon* appears to have been correctly placed within the Eubriinae, the distinctive dorsal morphology of the larva and its unique gill tuft number suggest that the genus separated from all other eubriine genera at a very early stage in its evolutionary history. A further discussion of this point is given in Chapter 4.

Systematics within the Psephenidae

The existence of two very different forms of respiratory structure in the Psepheninae and Eubrianacinae on one hand and the Eubriinae and Psephenoidinae on the other (Psepheninae and Eubrianacinae possessing

ventral tracheal gills, Eubriinae and Psephenoidinae with retractable anal tracheal gills) suggests an extremely early split in the evolution of these two groups. From a detailed examination of respiratory systems in both pupae and larvae, Hinton (1966) constructed a partial phylogeny for the family. This is based on the reduction of functional spiracles and the fact that this process appears to be an irreversible one making it possible to distinguish between permissible and impermissible derivations. Hinton (1966) found that the Psepheninae possess the least reduced respiratory system and that respiratory systems of the other three subfamilies can be derived from that system.

On the basis of the different tracheal gill structures within the family it can also be suggested that the Psepheninae and its apparent sister group, the Eubrianacinae, are more primitive forms than the Eubriinae and its apparent sister group, the Psephenoidinae. The presence of the retractable anal tracheal gills, which undergo active ventilation, in the Eubriinae and Psephenoidinae, can be considered to be an apomorphic feature. These gills allow the larvae to live in a wide range of lotic habitats, in particular those experiencing variable flow regimes. In contrast, the larvae of the Psepheninae and Eubrianacinae possess the apparently plesiomorphic ventral tracheal gills, which do not undergo active ventilation, and so they are restricted to permanent, moderate to fast flowing rivers and streams.

The similarity found between several features of the dorsal surface of the larvae of *Sclerocyphon* and the larvae of the Psepheninae and Eubrianacinae (presented in the two previous sections) is regarded, in this study, as evidence of a common, although very distant, ancestor. This study, therefore, albeit limited to only one genus, supports Hinton's (1955) classification of the Psephenidae in which the Eubriinae

are accorded sub-familial status, rather than Bertrand's (1956) classification which places the taxon at the level of family.

Bertrand's (1972) later classification, in which he creates three families from the four psephenid subfamilies previously recognised can be criticised on its apparent lack of conformity to the concept of the family category. Mayr (1969) considers the "family" to represent,

> "a monophyletic group of genera which is separated from other families by a decided gap".

He recommends that the size of the gap should be in an inverse ratio to the size of the family and that the family can be distinguished,

> "by certain adaptive characters which fit it for a particular niche or adaptive zone".

Certainly the four subfamilies display common adaptive characters for their life as members of the stone fauna in lotic communities. Bertrand (1972) provides little evidence in support of a polyphyletic, as opposed to monophyletic, derivation of the genera involved and his classification creates three very small families separated by very small gaps.

The most critical factor in accepting or rejecting Bertrand's (1972) classification, however, is the argument as to whether the similar features exhibited by the larvae of the four subfamilies (in particular the dorso-ventrally flattened shield and attendant features of the dorsal surface) represent synapomorphy or merely convergence, as assumed by Bertrand. Therein lies the strength of Hinton's interpretation of psephenid phylogeny based on the presence of functional and non-functional spiracles and in the words of Mayr (1969) giving

"an indication of an underlying basis genetic similarity" rather than more specialised adaptations to a particular environment.

Obviously more information on both the adults and the larvae of various species, in particular, the relatively unknown species of Africa, South America and Asia, is needed before the debate on pseph-enid phylogeny can be resolved.

PART TWO

CHAPTER FOUR

DISTRIBUTION AND ZOOGEOGRAPHY

4.1 Introduction

Zoogeography may be defined as the study of patterns of animal distributions in time and space. Implicitly, such a study aims to explain, rather than merely catalogue, distributions.

The main questions to be answered in the present study are

1. What are the distribution patterns of species of *Sclerocyphon*?

2. How may these distributions be explained?

Platnick and Nelson (1978, p.1) state that

> "...historical explanations of biotic distribution patterns fall into two classes, dispersal explanations and vicariance explanations."

In dispersal models, disjunctions in animal distributions are explained by the occurrence of dispersal across pre-existing barriers while in vicariance models disjunctions are explained by the appearance of barriers fragmenting the ranges of ancestral species.

Much debate has taken place, in the past five years, on the validity of each model. The vicariance model is favoured by many biogeographers as it enables hypotheses to be developed which are testable or falsifiable and thus represent scientific explanations, *sensu* Popper (1959). Hypotheses developed using the dispersal model are not falsifiable but McDowell (1978, p.340) suggests that the dispersal model should still be included in biogeographical models "for the sake of a more realistic, even if less rigorous theory".

The appropriateness of either model would seem to depend very much upon the group(s) of animals, and, in particular, upon the vagility of the group(s), under consideration. As Thornton (1980, p.265) has noted

> "...the fact that one type of event...
> *vicariance or dispersal* ... has occurred
> does not logically exclude the possibility
> of the other..."

and it seems likely that both contribute to the majority of distributions.

Both models will be employed, in the present study, in an attempt to explain the distributions of *Sclerocyphon*.

An important component of many vicariance models is the theory of continental drift, or its more recent extension, plate tectonics, and it is only in the last 15 years that this theory has received universal recognition and acceptance. Wegener's theory was first published in 1912 and although Du Toit expanded upon it in 1937, it was the subject of controversy and disbelief for many years. Not until the 1960's when evidence of the past positions of continents was provided by palaeomagnetic data, and studies of ocean floors revealed a mechanism for drift (sea-floor spreading) did the theory achieve widespread acceptance (Smith, 1974).

Prior to the acquisition of geological evidence in support of continental drift some zoologists, including Illies (1965), Brundin (1966) and Ross (1967) believed that the disjunct distribution patterns of several freshwater insect groups were evidence of past land connections linking South America with Australia - New Zealand through Antarctica.

The basic tool of zoogeography is taxonomy (Mackerras, 1970) and many workers including Brundin (1966), Ross (1967), Edmunds (1972), Nelson (1973), Ball (1975), Platnick and Nelson (1978), McDowell (1978, 1980) and Zwick (1981) have emphasised the importance of basing zoogeographical analysis on strictly phylogenetic (cladistic) classifications. Zwick (1981) notes that phylogenetic analysis is a historical science in that it is concerned with the reconstruction of genealogies, and there-

fore represents the only valid partner of historical biogeography.

Although the phylogeny of the Psephenidae is still under debate (Chapter 3), the proposed phylogeny of *Sclerocyphon* presented in this study (Chapter 3) does allow some comments to be made on the zoogeography of the genus.

A brief account of the Australian environment, past and present, is given, in the following section, to provide a basis for the discussion of factors which may have influenced the distribution of *Sclerocyphon* in Australia. The distributions of *Sclerocyphon* species and larval types described in Chapter 3 are documented and discussed in the light of the above knowledge. A general but brief account of the world-wide distribution of the Psephenidae is also given.

Figure 4.1 is a map of Australia on which the localities referred to have been marked. The term Australia is taken to mean both the Australian mainland and Tasmania. Cox *et al.* (1976) is the source of the geological time scale referred to in the following text.

4.2 The Australian Environment, Past and Present

Geological History

Much evidence now exists indicating that Australia, together with Antarctica, New Zealand, South America, Africa, India, Ceylon and Madagascar previously formed one southern supercontinent, Gondwanaland. Europe, northern Asia and North America formed a northern supercontinent, Laurasia. These two landmasses were intact and probably united, as Pangaea, at the beginning of the Triassic, 225 m.y. ago (Valentine and Moores, 1970). They separated during the early Mesozoic and large scale drifting of the continents has taken place since the Cretaceous (Smith, 1974).

The sequence of events in the break up of East Gondwanaland is

FIGURE 4.1 Map of Australia showing some localities referred to in the text.

summarised in a tectonic calendar compiled by Powell *et al.* (1981). The breakup commenced with the separation of Greater India, 125 m.y. ago. The rifting of the Austro-antarctic plate appears to have commenced in the Late Cretaceous, 80 m.y. ago, with New Zealand separating from West Antarctica and moving northwest.

The present regional geography of Australia is a result of the breakup and spreading out of a geosynclinal belt on the eastern margin of Gondwanaland (Raven and Axelrod, 1972). The Austro-antarctic plate started moving northwards in the Late Cretaceous and Australia separated from Antarctica in the Paleocene/Eocene, 55 m.y. ago. Until this time Australia had been linked with South America through Antarctica and these latter two continents remained in contact until the Oligocene, 29.3 m.y. ago. It was the northward movement of the South Tasman Rise, away from Antarctica, and the opening of Drake's Passage to oceanic currents, 23.5 m.y. ago, that allowed a circum-Antarctic current to form. This event was of major climatic importance as it represented the beginning of the modern role of Antarctica as a dominant force in determining the world's weather (Coleman, 1980).

Separation of Africa from South America had occurred earlier, 110 m.y. ago, while the separation of Africa from Antarctica probably occurred 90 m.y. ago (Raven and Axelrod, 1972).

Climatic History

The Tertiary

A review of the paleoclimatic and paleobotanical data relevant to Australia during the Tertiary has been presented by Kemp (1978, 1981). She suggests that the evolution of both the Australian and Antarctic environments over the last 60 m.y. are intimately linked. During that time Australia also underwent a steady northward drift, resulting in

it's passing through a range of climatic belts, the width and nature of which were also changing.

The early Tertiary in Australia was characterised by both widespread humidity and warmer temperatures than those now experienced (Kemp, 1978). Beard (1977) suggests that Australia experienced a humid non-seasonal climate during the Eocene and Gentilli (1961) believes that moister climates than today prevailed in Australia during most of the Tertiary. As a result of such climates rainforest vegetation dominated the Australian landscape from the Paleocene through to the Miocene (Kemp, 1978).

A significant drop in temperature occurred in southern hemisphere localities at the Eocene-Oligocene boundary, 40 m.y. ago (Frakes, 1978) and the circum-Antarctic current which developed close to the Oligocene-Miocene boundary (as described above) must have been a significant factor in reducing the efficiency of meridional heat transport between the equator and pole (Kemp, 1981).

During the Miocene Australia's climate was influenced by both the continued northward drift of the continent and a marked increase in the volume of ice in Antarctica (Kemp, 1981). Sea surface temperature determinations indicate that early Miocene seas were warmer than both the preceding Oligocene and present day temperatures and precipitation would have been high. In the late Miocene the Antarctic ice sheet underwent rapid expansion and this appears to have affected the Australian climate by both lowering temperatures and increasing dry, anticyclonic circulation (Kemp, 1981).

Raven and Axelrod (1972) consider that Australian desert and semi-desert regions developed in post-Eocene times as the continent moved into the world-wide belt of reduced precipitation at the edge of the tropics, "the horse latitudes". Bowler *et al.* (1976) suggest

that the trend towards aridity in Australia began in the middle Miocene. Galloway and Kemp (1981) consider the Pliocene to have been an important phase in a climatic change towards increasing aridity, although they note that climatic data for Australia during that epoch is sparse. Overall the Tertiary appears to represent a period of long-term climatic change in Australia, from widespread, warm tropical conditions to cooler climates and increasing aridity in the centre of the continent.

The Quatenary

The most recent epoch, the Pleistocene, has been a time of even more dramatic climatic changes than the Tertiary. During the Early and Middle Pleistocene Australia was influenced by world-wide changes in sea level and climate. The climate appears to have been predominantly dry but, as yet, very little paleoclimatic data is available for that time. More information is available on the Late Pleistocene and Holocene climates and Bowler *et al.* (1976) have provided a comprehensive account of these.

Between 60,000 and 40,000 years ago conditions in Australia were drier and possibly colder than today. Tasmania and to a lesser extent, the Snowy Mountains, had a late Quaternary (25,000 - 15,000 years ago) glacial episode that may have been equivalent to the late Würm-Wisconsin glaciation of the northern hemisphere. This was a period of both low temperatures and great aridity in Australia. Between 15,000 and 10,000 years ago temperatures rose rapidly and most of the ice disappeared. In the last 10,000 years the climate has been relatively stable although a period of higher rainfall and warmer conditions than present occurred 6-9,000 years ago (Bowler *et al.*, 1976).

Galloway and Kemp (1981) believe that changes comparable to those of the last 40,000 years occurred repeatedly throughout the Pleistocene

and note that, throughout the Late Cainozoic, dry conditions appear to coincide with low temperatures and wet conditions with warmer temperatures.

Land Connections Between the Australian Mainland and Tasmania

Tasmania is presently separated from the Australian mainland by Bass Strait, a strip of water at its narrowest point only 240 km wide and at its shallowest less than 70 m deep (Williams, 1974). Bass Strait is a flooded NW-SE trending elliptical graben which originated about 65 m.y. ago, during the separation of Australia and Antarctica (Griffiths, 1971).

Tasmania first became isolated from the Australian mainland with the flooding of Bass Strait during the Miocene but was later reconnected for a period, during the Pliocene, by an eastern land bridge passing through Flinders Island to Victoria (Williams, 1974).

Sea levels fluctuated repeatedly through more than 200 metres during the Pleistocene (Galloway and Kemp, 1981) as a consequence of which Tasmania and the Bass Strait Islands were connected to the mainland several times by an extensive landbridge. It appears that Tasmania was last linked to the mainland between 22,500 and 12,750 years ago (Rawlinson, 1974) a period during which southern Australia experienced a full glacial climate.

Physiography

Australia, consisting of the Australian mainland (7,614,500 square kilometres) and Tasmania (67,800 square kilometres) lies between the latitudes 10 degrees and 40 degrees south.

Three physical subdivisions are recognised in the continent; the Western Plateau or Western Shield, the Central Lowlands or Central Basin, and the Eastern Highlands (Figure 4.2). The Western Plateau

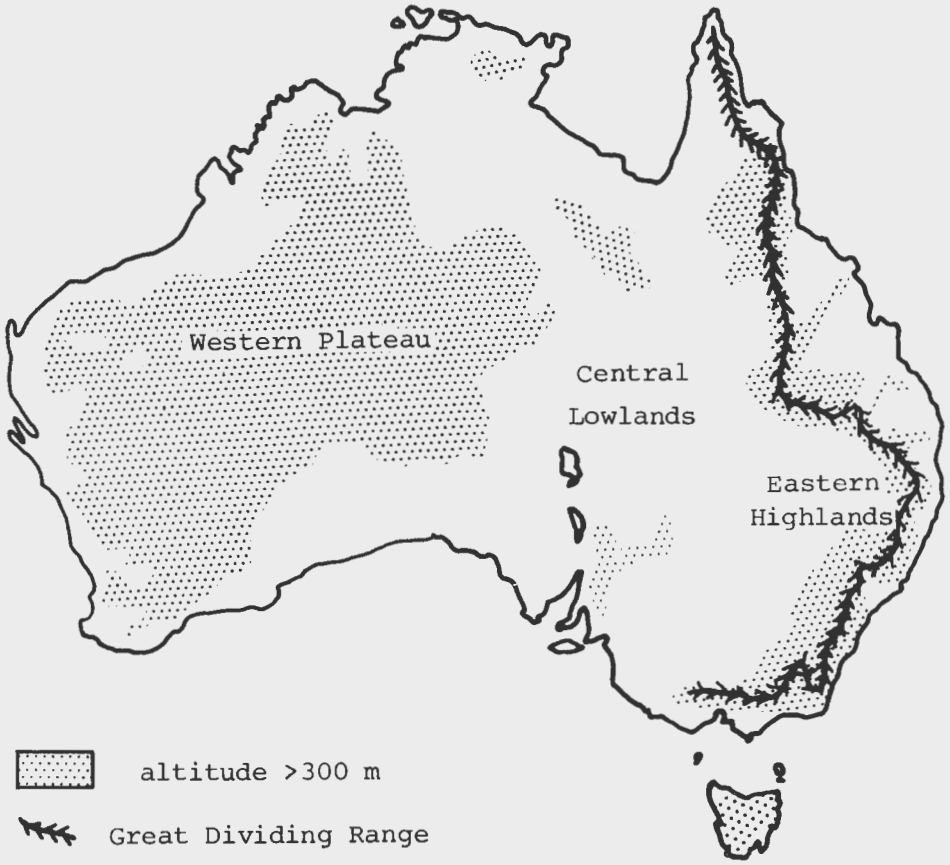


FIGURE 4.2 Major physical subdivisions of Australia and the Great Dividing Range.

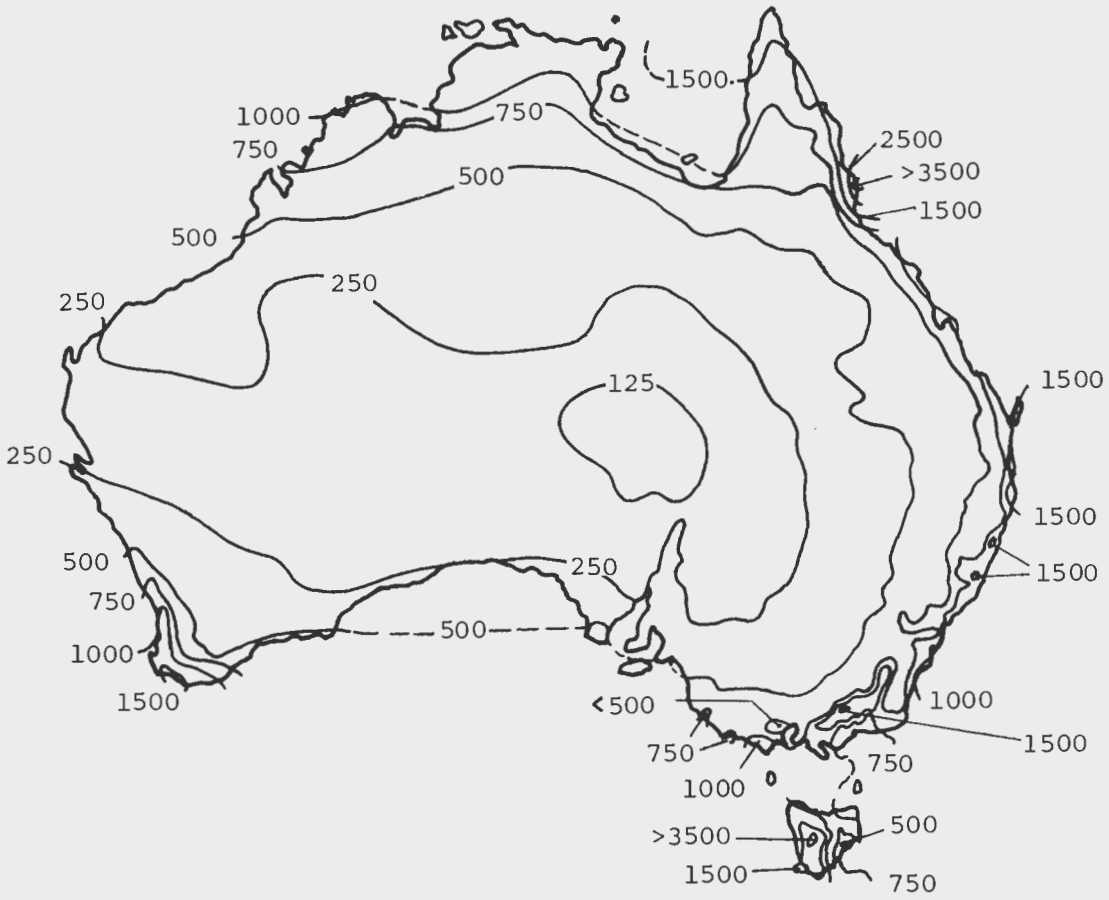


FIGURE 4.3 Map of rainfall in Australia (after Gentilli, 1972).

extends over the western half of the continent and is a vast flat surface of moderate elevation mostly between 200-500 m above sea level. The Central Lowlands is composed of two large sedimentary basins and smaller associated basins characterised by low relief and very low gradients. The Eastern Highlands form an elevated strip extending from north to south parallel to the eastern seabord and including the Bass Strait Islands and Tasmania. An east-west spur is present in Victoria extending from the Victorian Alps to the Grampians in western Victoria. The Great Dividing Range is the predominant feature of the Eastern Highlands on the Australian mainland. The Great Dividing Range (illustrated in Figure 4.2) is so named because it forms an important divide between the shorter east coast rivers and the extensive river systems of the Murray-Darling and Carpentaria Basins to the west.

The Eastern Highlands correspond to the Eastern Orogenic Province (Nix, 1981) and are a result of tectonic movements which commenced in the Mesozoic and continued through to the Tertiary. These movements broadly coincided with the breakup of Gondwanaland and the separation of the Australian-Antarctic plate. Nix (1981) notes that various lines of evidence suggest that the present configuration of upland areas and drainage patterns is much the same as that that existed by the early to mid Tertiary.

Altitudes in the Great Dividing Range extend from 500 to 1,000 m with individual mountains exceeding 1,500 m in Tasmania, the Victorian Alps, the Snowy Mountains, the New England region and north Queensland. The highest peak in Australia is Mt. Kosciusko, at 2 228 m, in the Snowy Mountains (Nix, 1981).

Climate

Rainfall

The overall pattern of rainfall distribution in Australia has been described as a series of concentric zones of steadily increasing rainfall spreading outwards from a vast central arid region (Keast, 1959). A map of the average annual rainfall in Australia (after Gentilli, 1972) is given in Figure 4.3. The actual distribution of rainfall throughout the year changes between northern and southern Australia. In the north rainfall is a predominantly summer phenomenon, in the eastern strip between Rockhampton and Victoria rainfall is well distributed throughout the year, while in the southernmost part of mainland Australia and Tasmania rainfall is at a maximum in winter. A more detailed rainfall map for Tasmania is given in Chapter 5.

Temperature

In Australia temperatures are mainly controlled by latitude but may be considerably modified by altitude (Gentilli, 1972). In the northern half of Australia, temperatures are high during most of the year with summer maxima usually over 38°C (100°F). In the southern half, temperatures vary considerably but average temperatures are more moderate (Gentilli, 1972).

Climatic Zones

The combined effects of rainfall distribution and temperature regimes on the Australian environment are best illustrated by the delineation of climatic zones. The Australian climate has been represented as a number of different zones by different workers. The climatic indices of Thornwaite (1933) and Köppen (1936) are most widely used throughout the world. Thornwaites' (1933) method of climate classification is followed in the present study and Thornwaites' zonation of the Australian

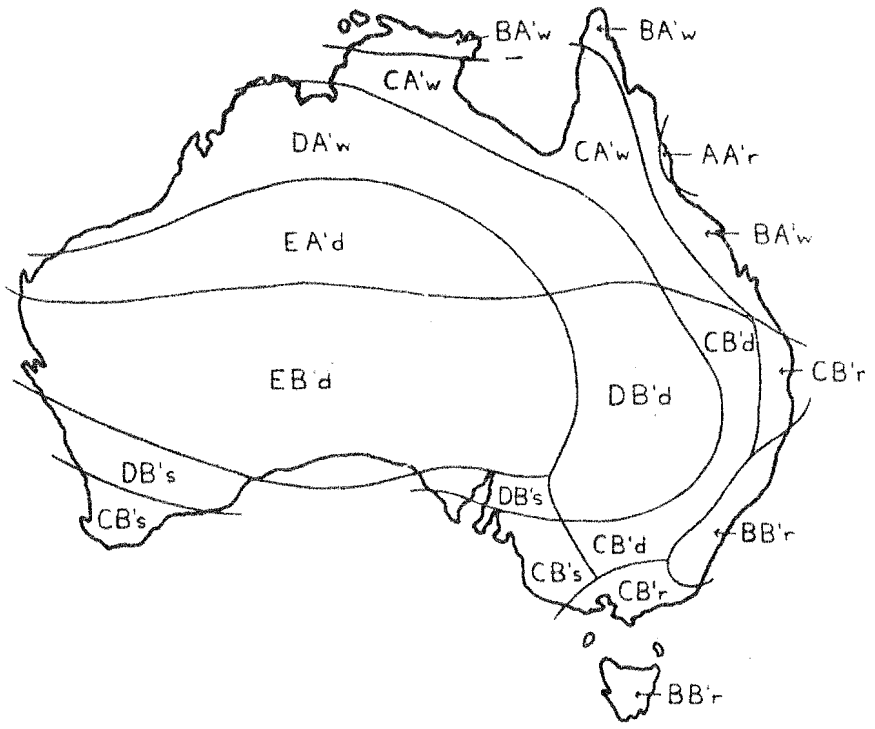


FIGURE 4.4 Climatic zones in Australia by Thornwaites' (1933) classification (after Keast, 1959).

A A'r Humidity: wet. Temperature: tropical. Vegetation: Rainforest. Rainfall abundant at all seasons.

B A'w Humidity: humid. Temperature: tropical. Vegetation: Forest. Rainfall deficient in winter.

B B'r Humidity: humid. Temperature: mesothermal. Vegetation: Forest. Rainfall abundant at all seasons.

C A'w Humidity: subhumid. Temperature: tropical. Vegetation: Grassland. Rainfall deficient in winter.

C B'r Humidity: subhumid. Temperature: mesothermal. Vegetation: Grassland. Rainfall abundant at all seasons.

C B's Humidity: subhumid. Temperature: mesothermal. Vegetation: Grassland. Rainfall deficient in summer.

C B'd Humidity: subhumid. Temperature: mesothermal. Vegetation: Grassland. Rainfall deficient in all seasons.

D A'w Humidity: semiarid. Temperature: tropical. Vegetation: Steppe. Rainfall deficient in winter.

D B's Humidity: semiarid. Temperature: mesothermal. Vegetation: Steppe. Rainfall deficient in summer.

D B'd Humidity: semiarid. Temperature: mesothermal. Vegetation: Steppe. Rainfall deficient in all seasons.

E A'd Humidity: arid. Temperature: tropical. Vegetation: Desert. Rainfall deficient in all seasons.

E B'd Humidity: arid. Temperature: mesothermal. Vegetation: Desert. Rainfall deficient in all seasons.

climate is illustrated in Figure 4.4. This figure, however, must be regarded as a large scale, general classification of climatic zones. Considerably more detailed descriptions can be drawn up, as illustrated by a climatic map of Tasmania constructed by Gentilli (1972, p.254) using Thornwaites' method.

From Figure 4.4 it can be seen that Australia's climatic zones lie in an approximately parallel series from north to south and grade into each other. A zone of particular interest is the Atherton-Cairns-Innisfail region of northern Queensland. This region is unique to Australia in that it experiences warm temperatures and abundant rainfall throughout the year. This region is regarded as the wettest of the Australian mainland (Gentilli, 1972). Innisfail receives over 600 mm in one month, March, 2,560 mm in the five months from December to April and more than 3,500 mm in the entire year. An extensive region on the west coast of Tasmania also receives over 2,000 mm per annum with one locality, Lake Margaret, receiving an average yearly rainfall of 3,683 mm (Gentilli, 1972), however, the temperatures of this region are cool temperate, rather than warm.

4.3 Distribution of Australian *Sclerocyphon*

The distribution of *Sclerocyphon* species and larval types, described in Chapter 3, are presented in Figures 4.5 - 4.23. Data pertaining to the collection of specimens in each species is provided under "Material Examined" (Chapter 3) and in Appendix A. The number of records of each species is marked in the left hand corner of each map. Where localities occur very close together some have not been marked on the map.

Sampling in Tasmania and Victoria was fairly extensive and thus a lack of records of *Sclerocyphon* from any particular region of these two States is seen as reflecting a real absence. Sampling elsewhere in

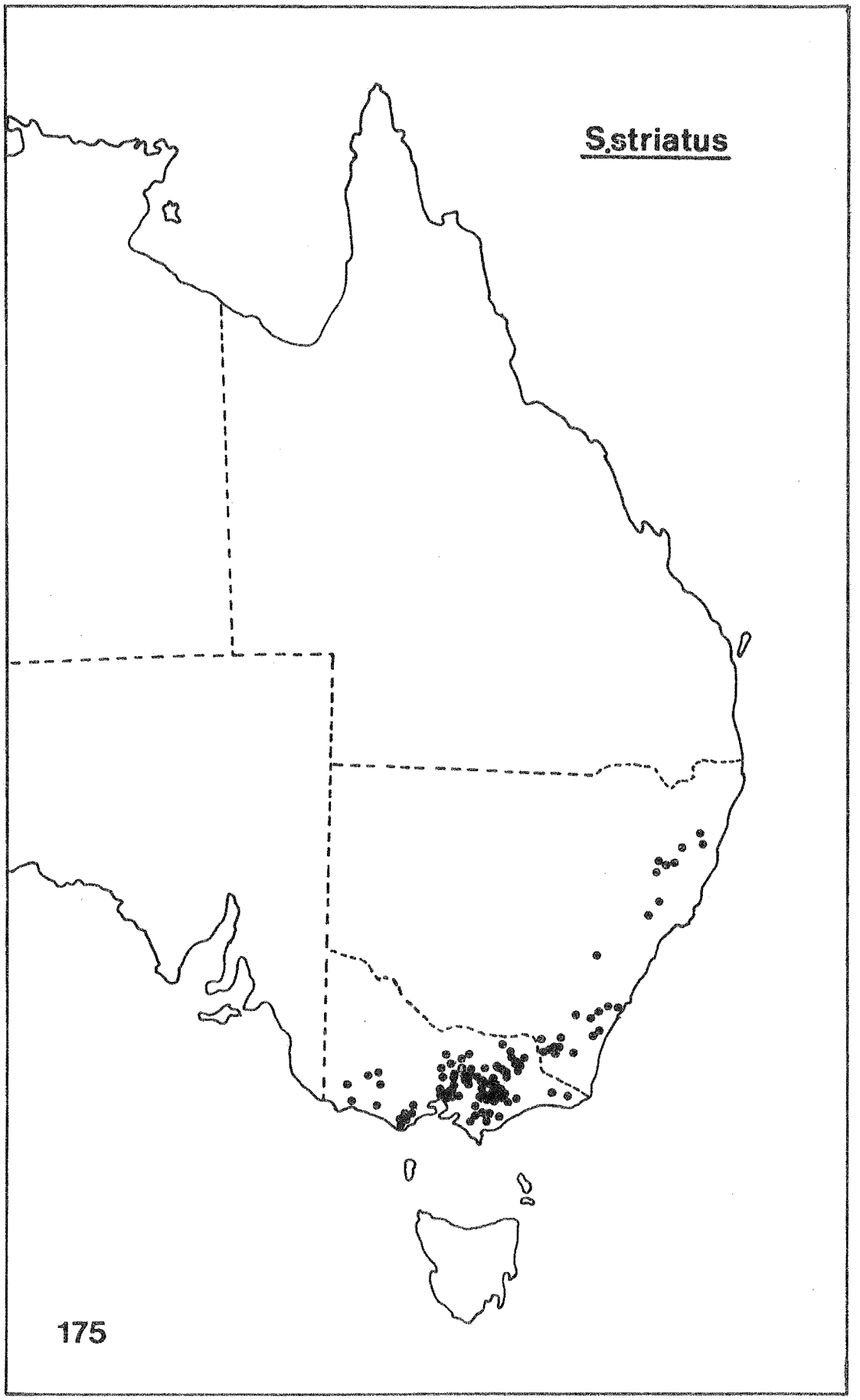


FIGURE 4.5 Distribution of *Sclerocyphon striatus*. Total number of records is shown at lower left.

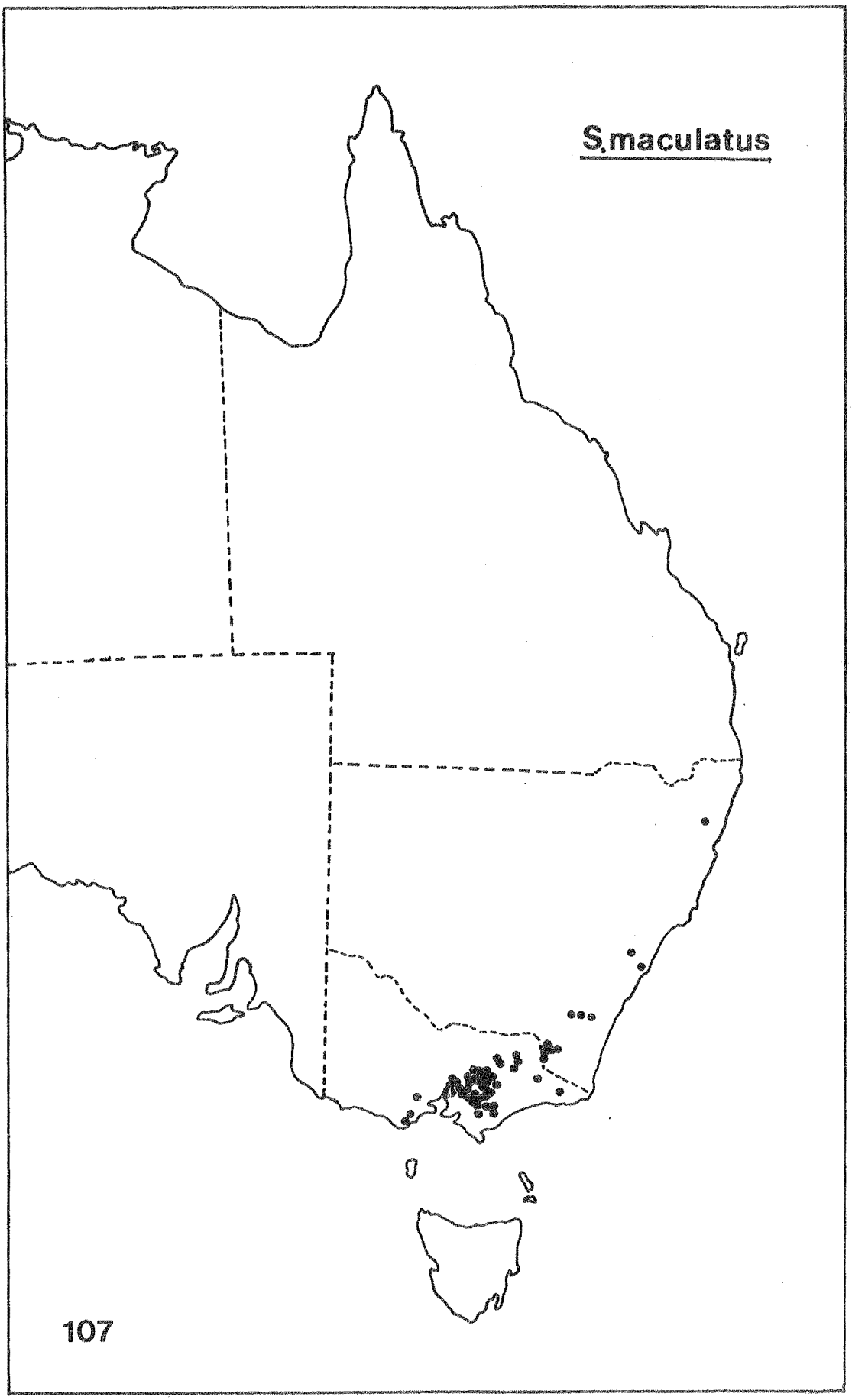


FIGURE 4.6 Distribution of *Sclerocyphon maculatus*. Total number of records is shown at lower left.

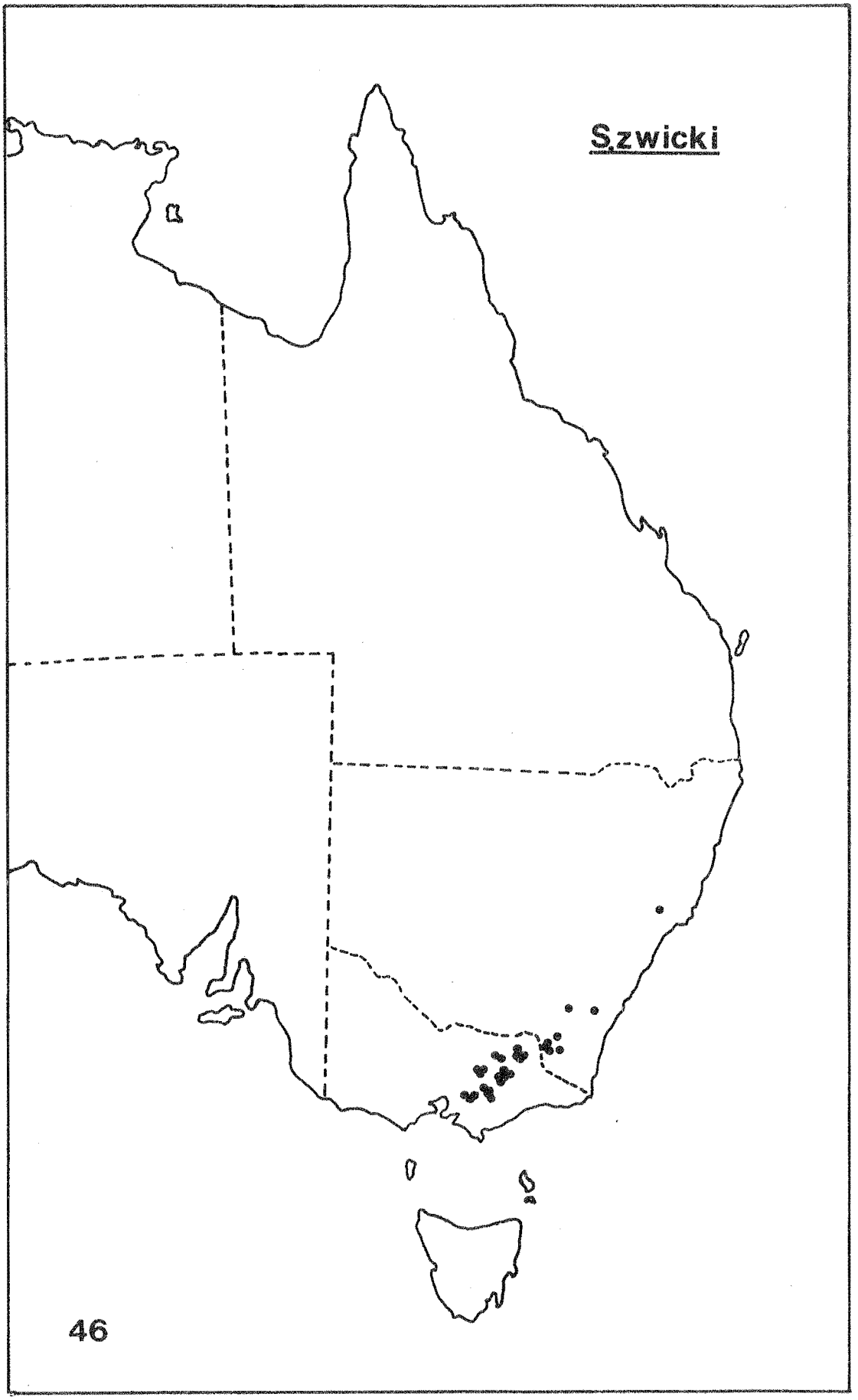


FIGURE 4.7 Distribution of *Sclerocyphon zwicki*. Total number of records is shown at lower left.

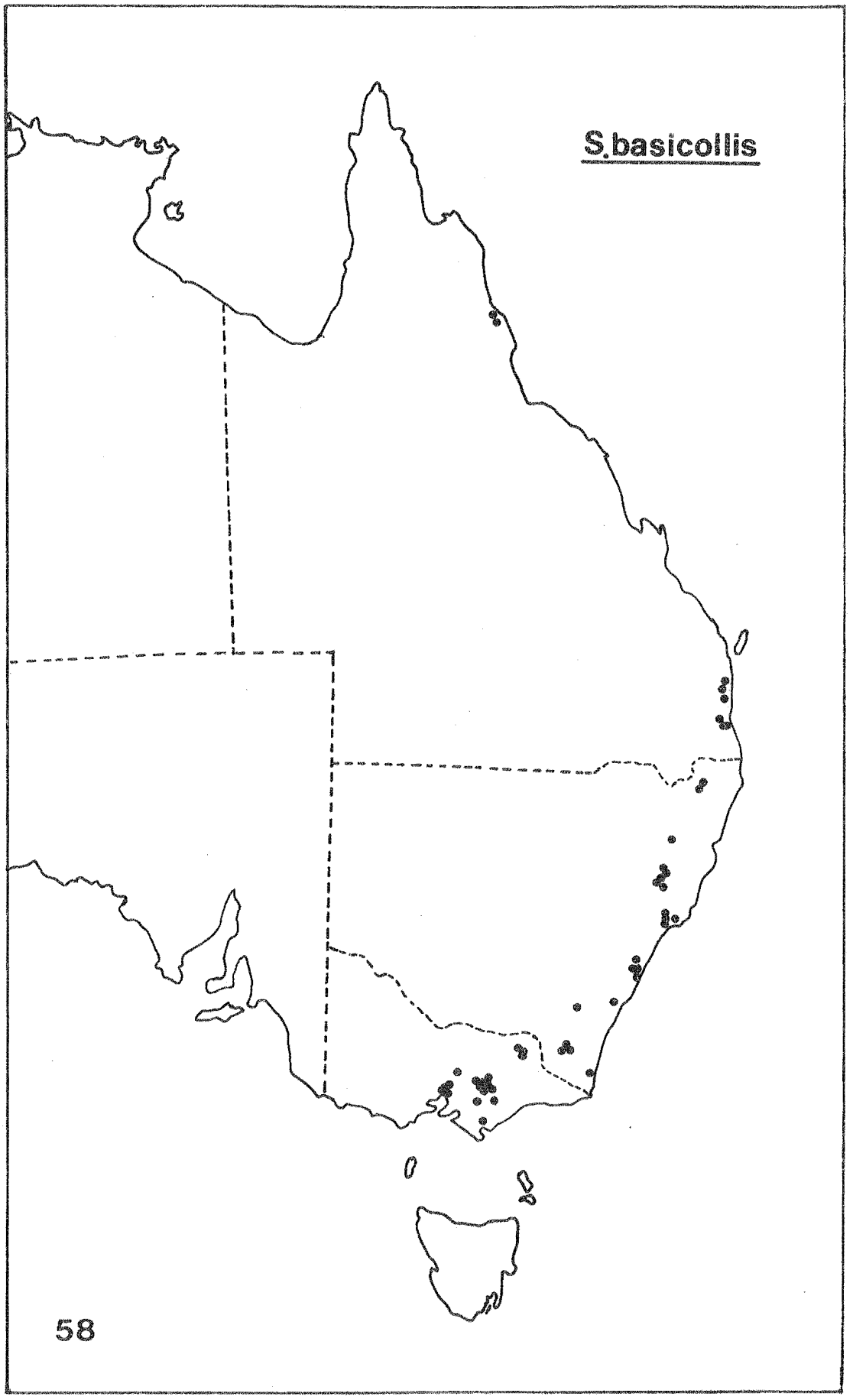


FIGURE 4.8 Distribution of *Sclerocyphon basicollis*. Total number of records is shown at lower left.

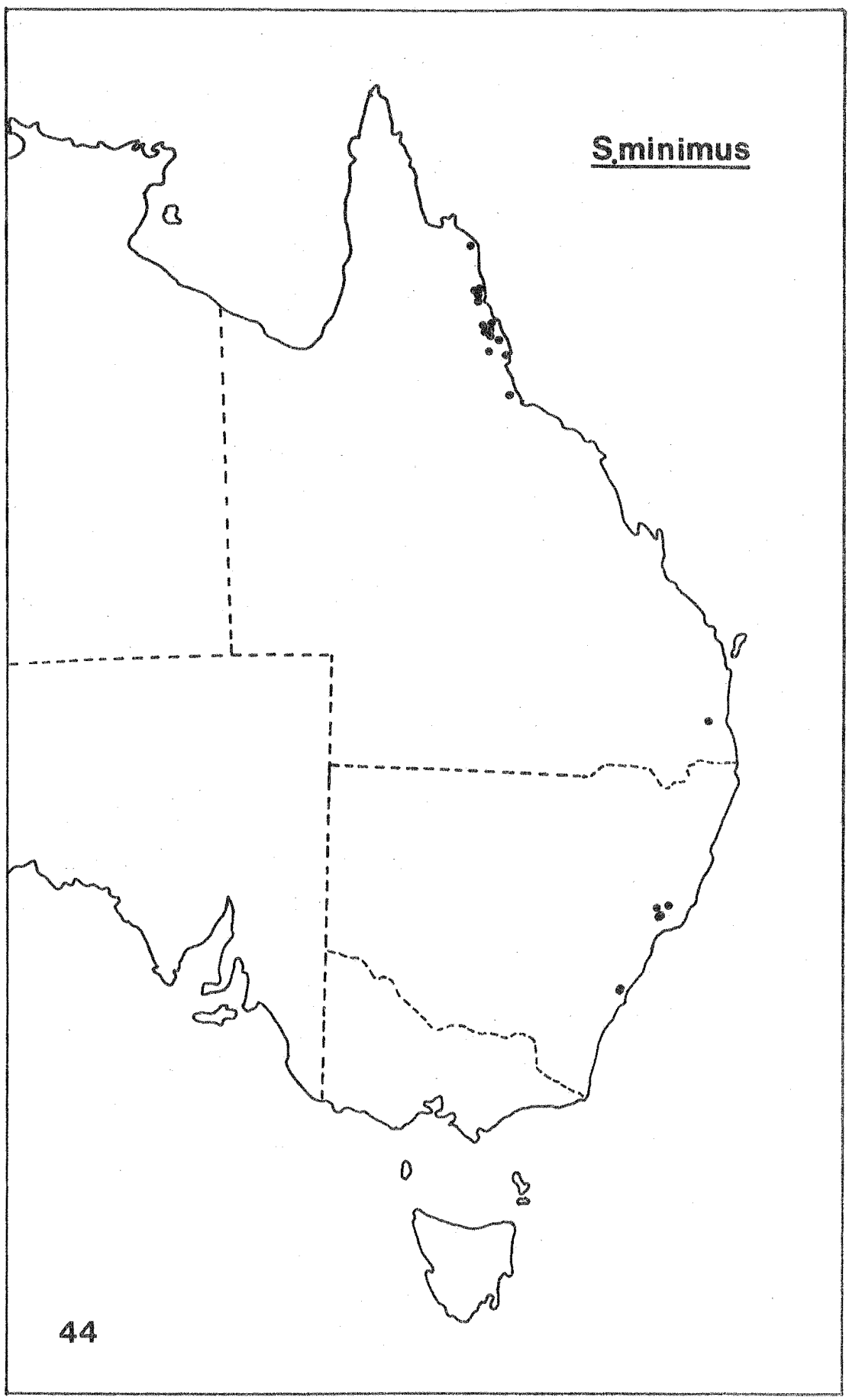


FIGURE 4.9 Distribution of *Sclerocyphon minimus*. Total number of records is shown at lower left.

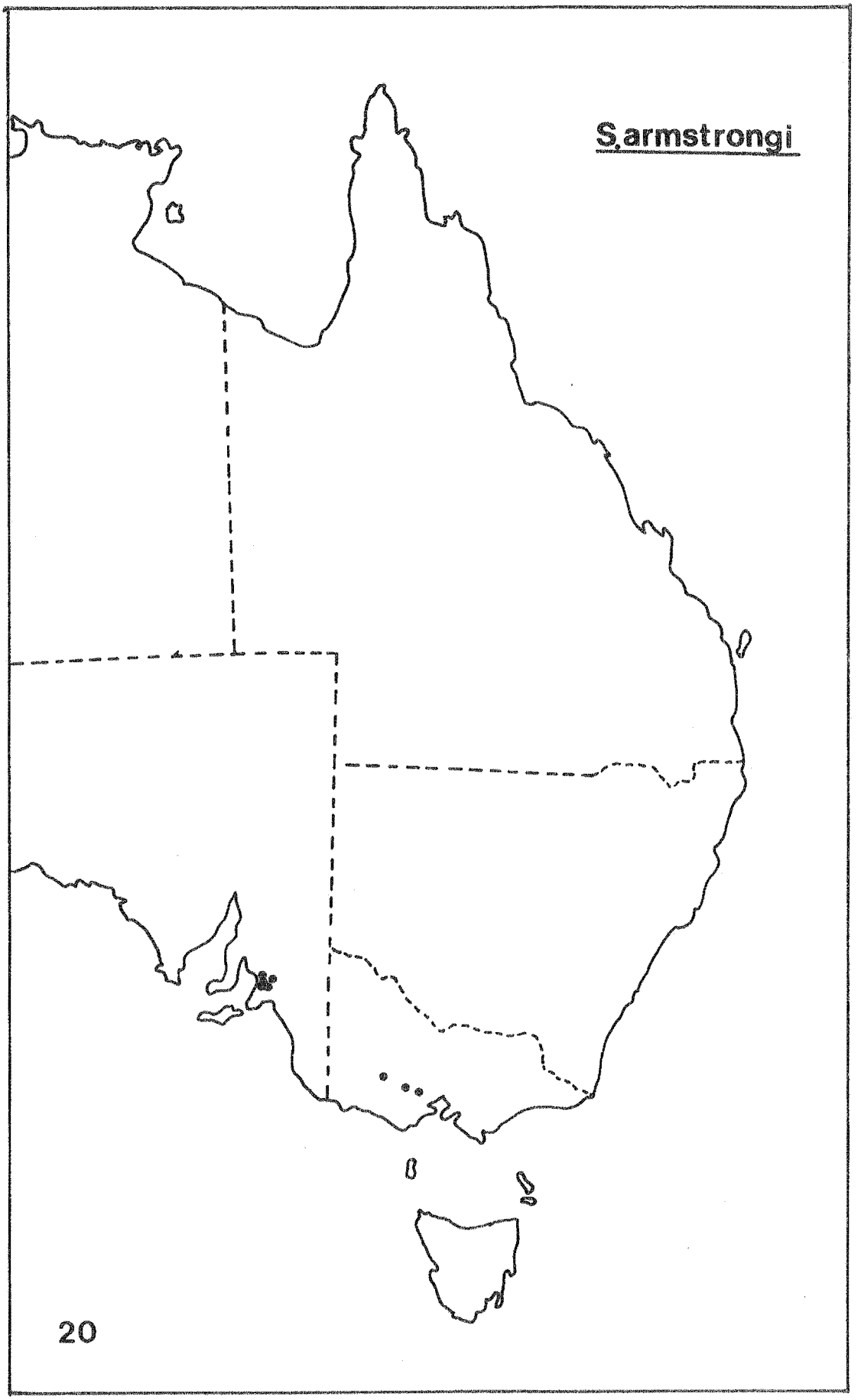


FIGURE 4.10 Distribution of *Sclerocyphon armstrongi*. Total number of records is shown at lower left.

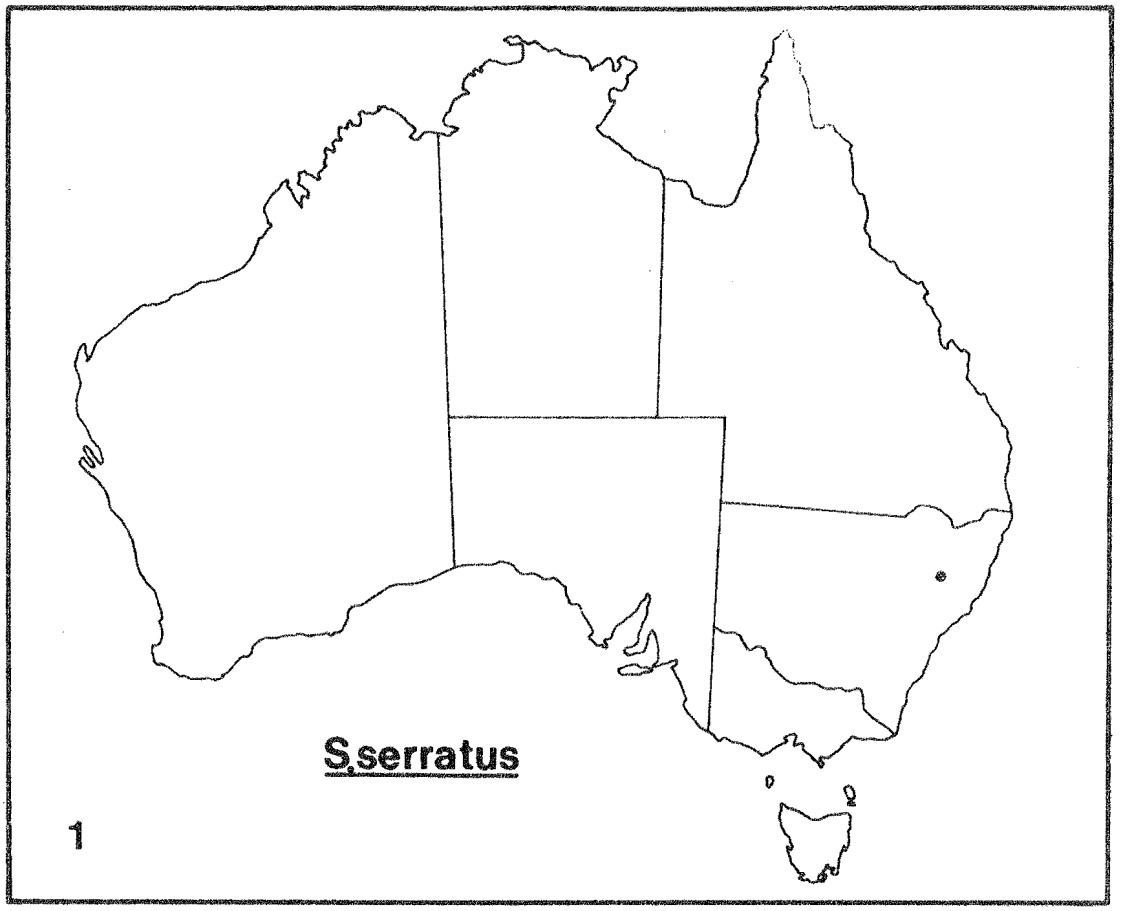


FIGURE 4.11 Single record of *Sclerocyphon serratus*.

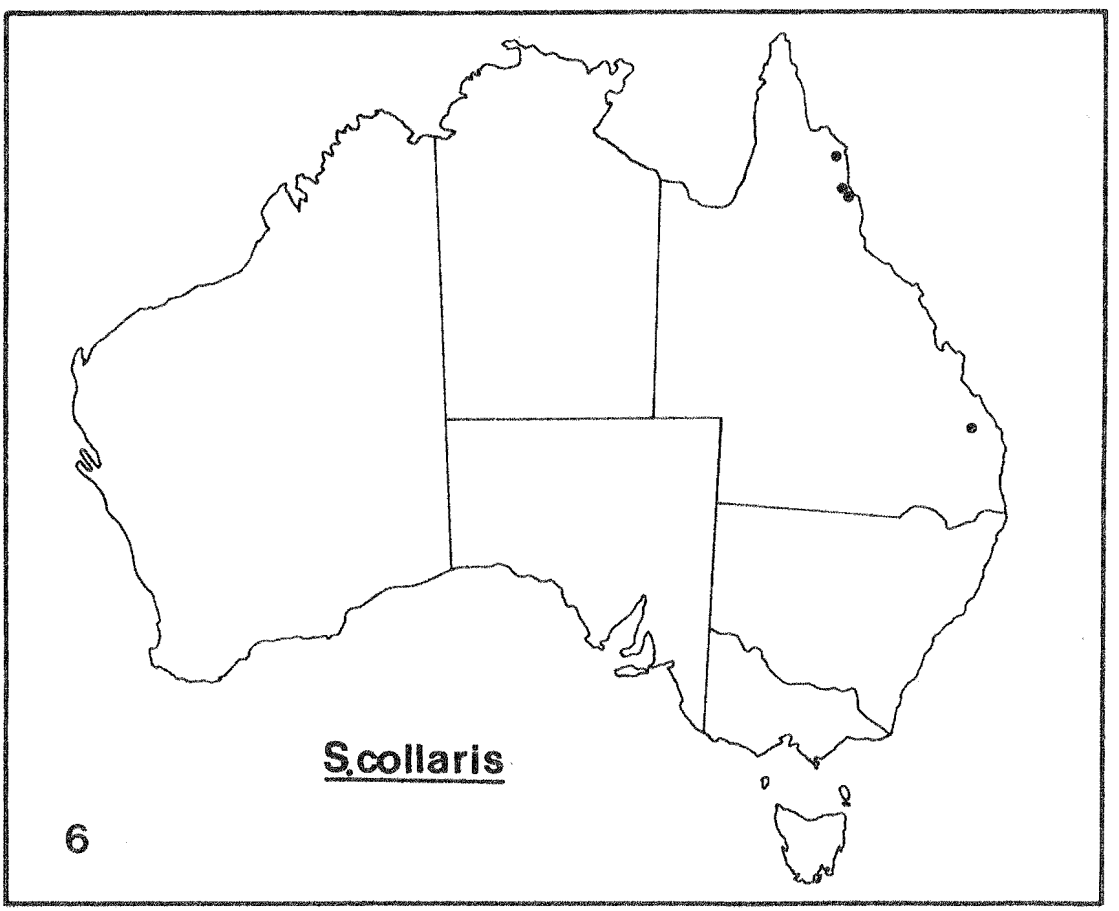


FIGURE 4.12 Records of *Sclerocyphon collaris*. Total number of records is shown at lower left.

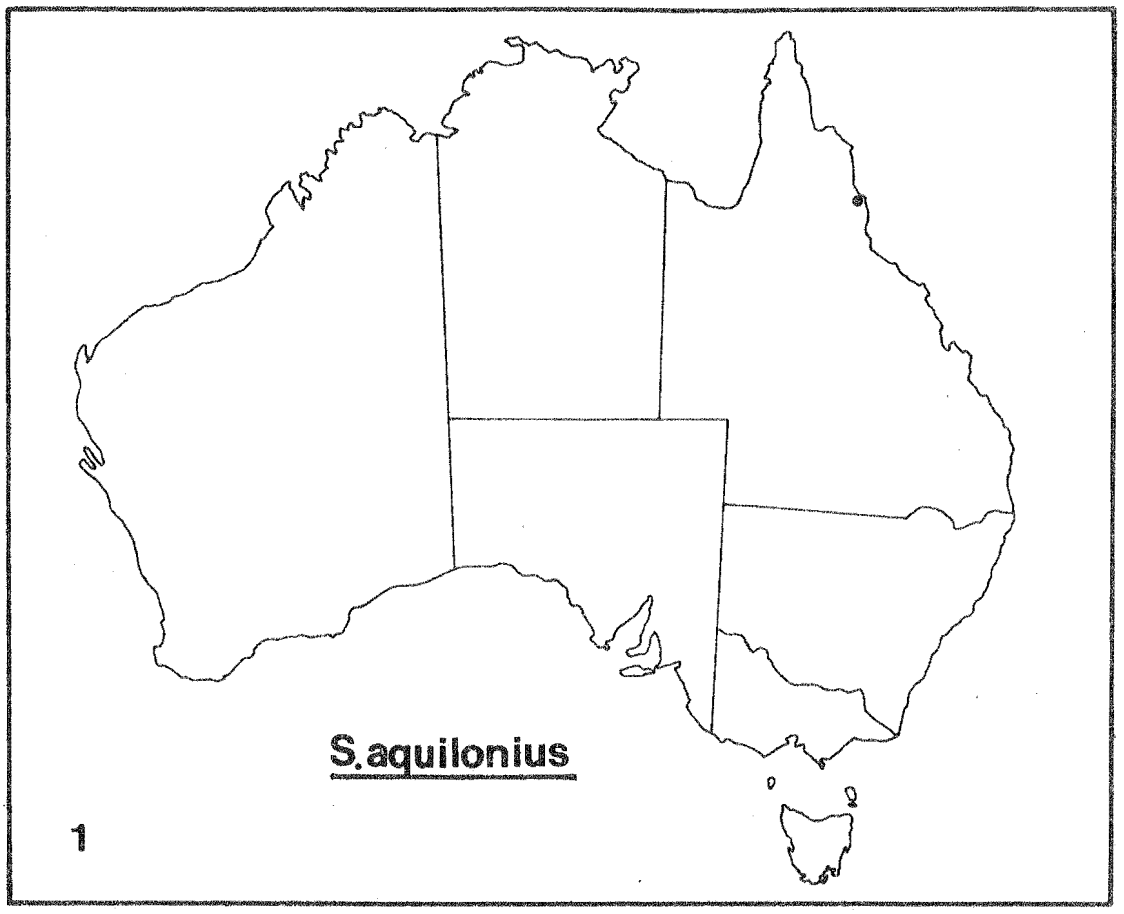


FIGURE 4.13 Records of *Sclerocyphon aquilonius*. Total number of records is shown at lower left.

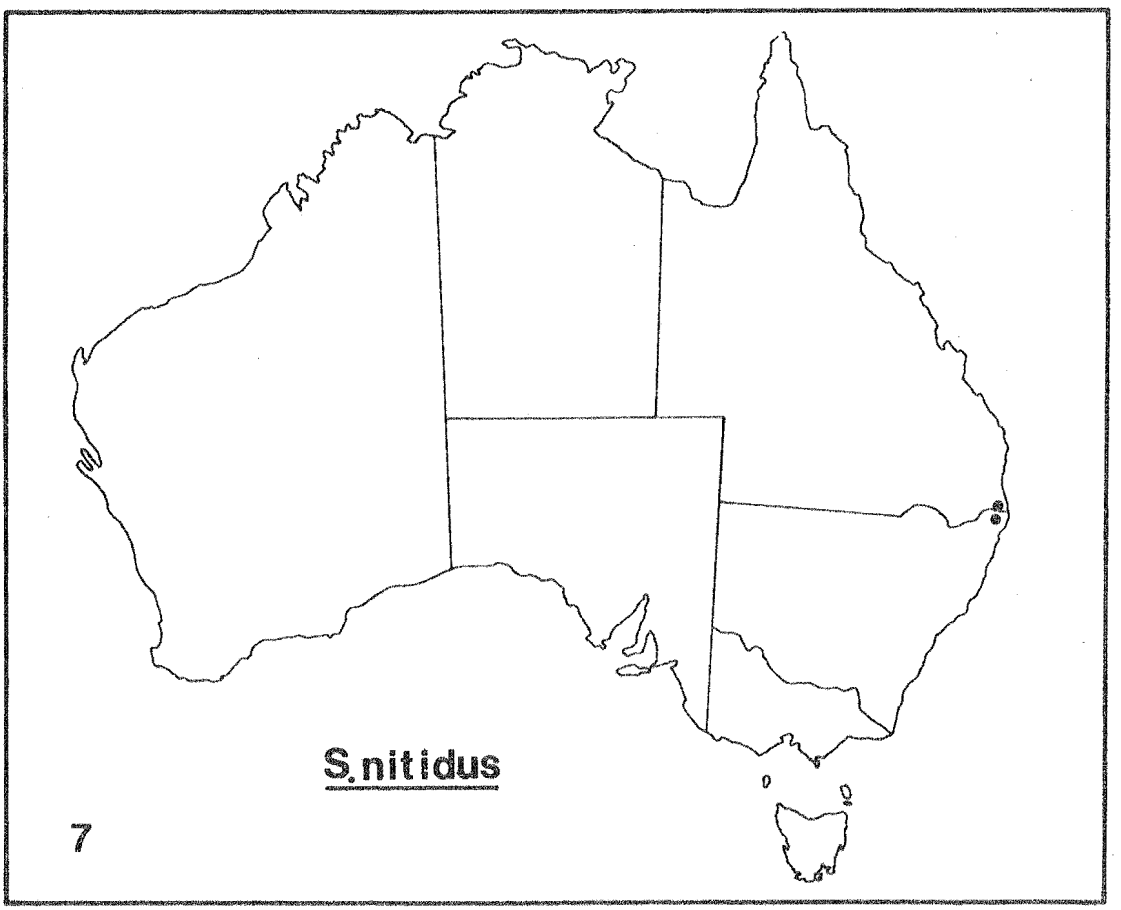


FIGURE 4.14 Records of *Sclerocyphon nitidus*. Total number of records is shown at lower left.

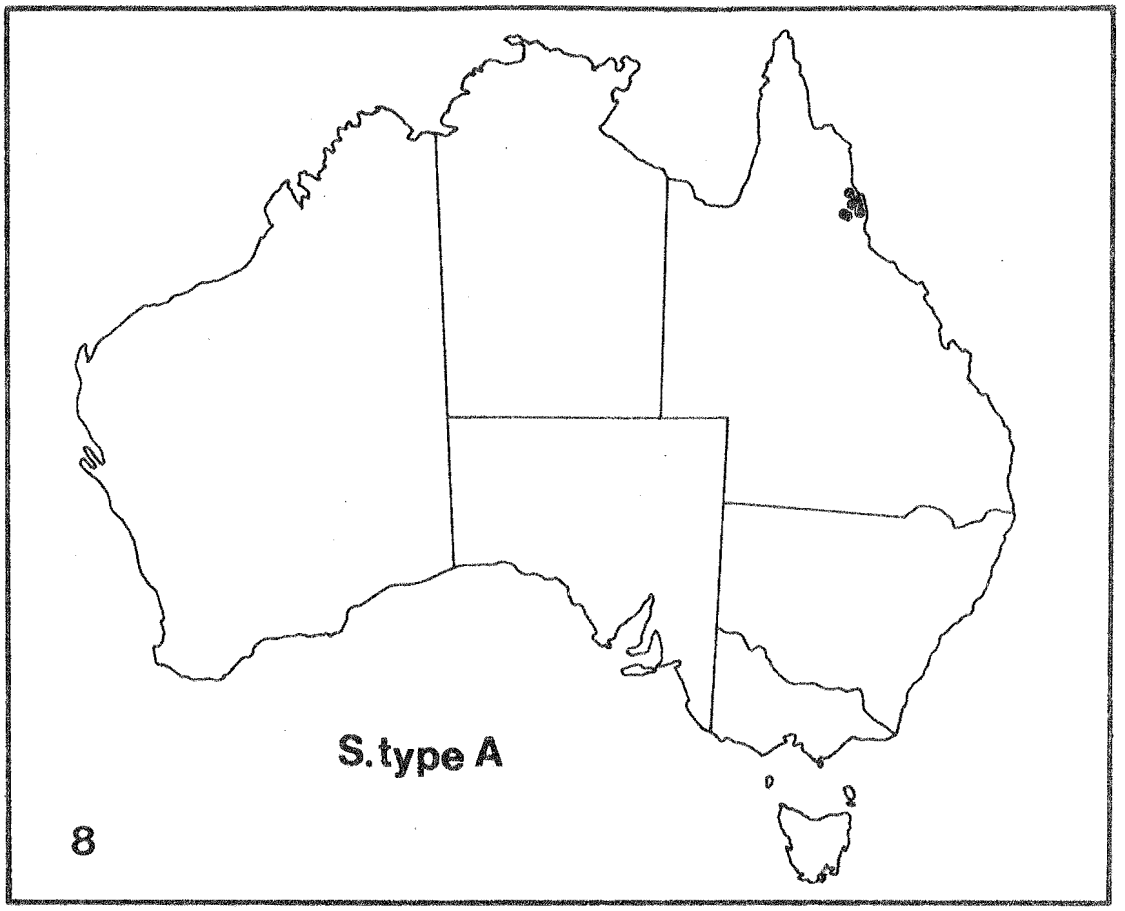


FIGURE 4.15 Records of *Sclerocyphon* type A. Total number of records is shown at lower left.

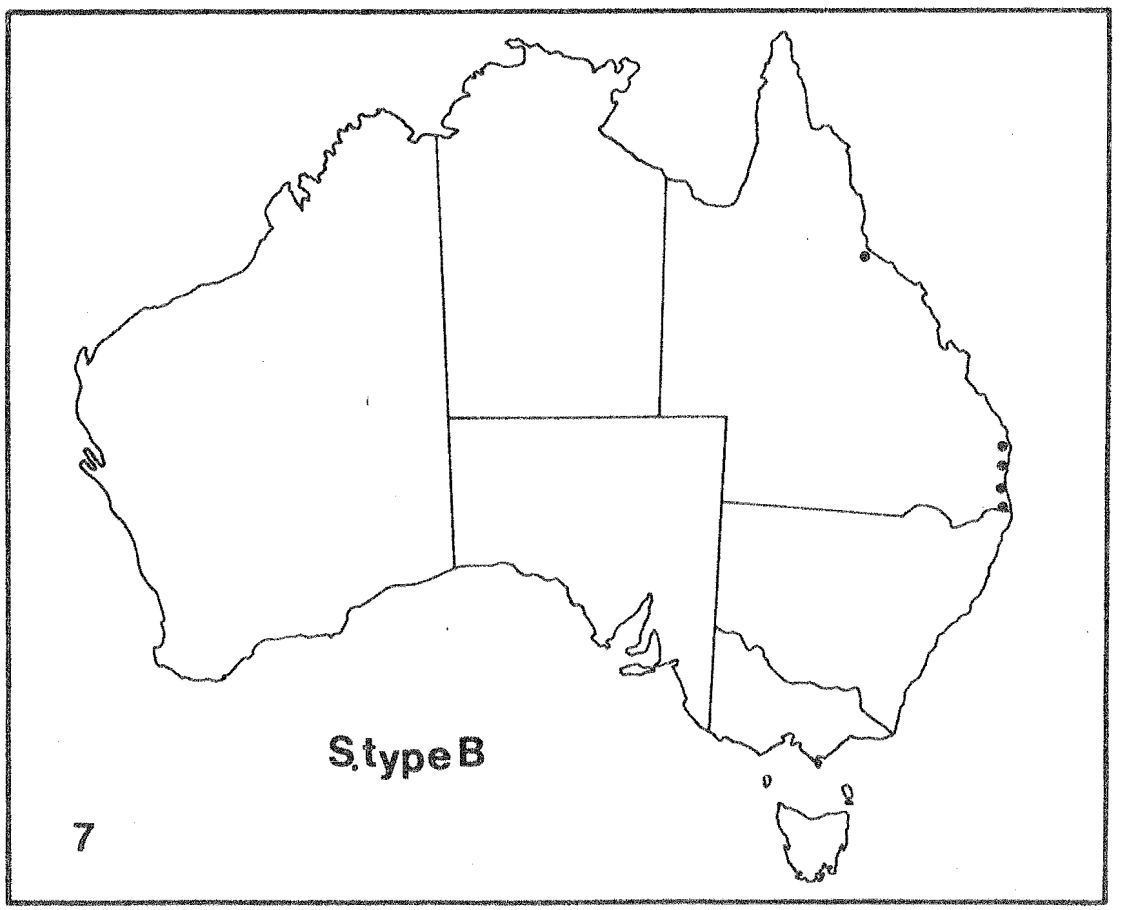


FIGURE 4.16 Records of *Sclerocyphon* type B. Total number of records is shown at lower left.

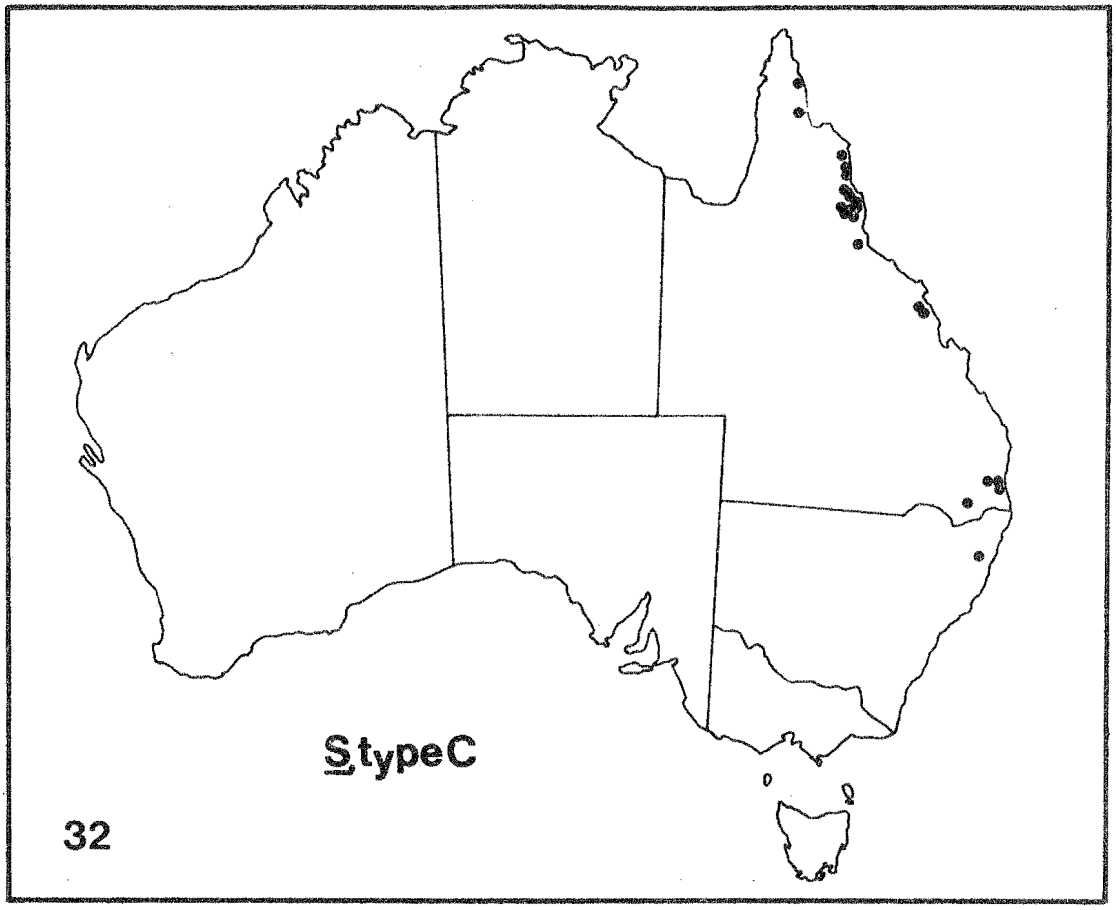


FIGURE 4.17 Records of *Sclerocyphon* type C. Total number of records is shown at lower left.

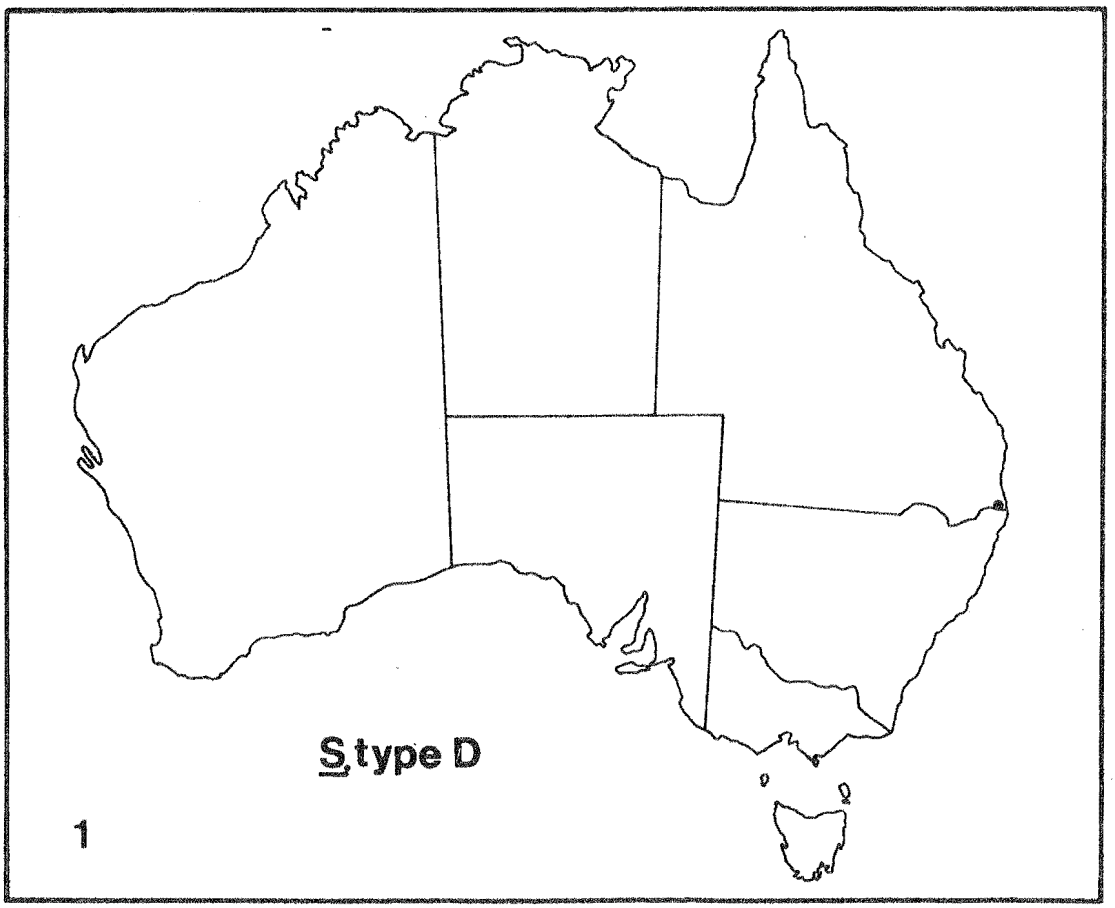


FIGURE 4.18 Single record of *Sclerocyphon* Type D.

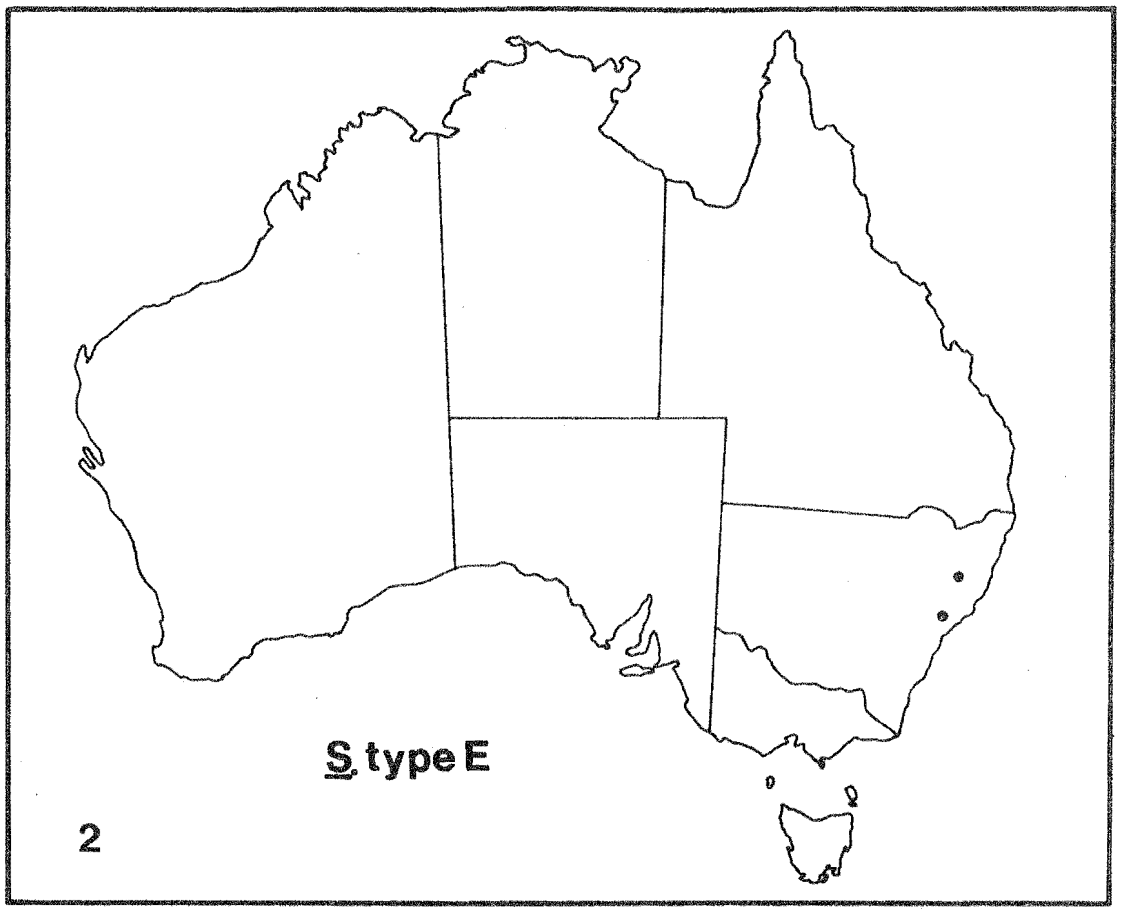


FIGURE 4.19 Records of *Sclerocyphon* type E. Total number of records is shown at lower left.

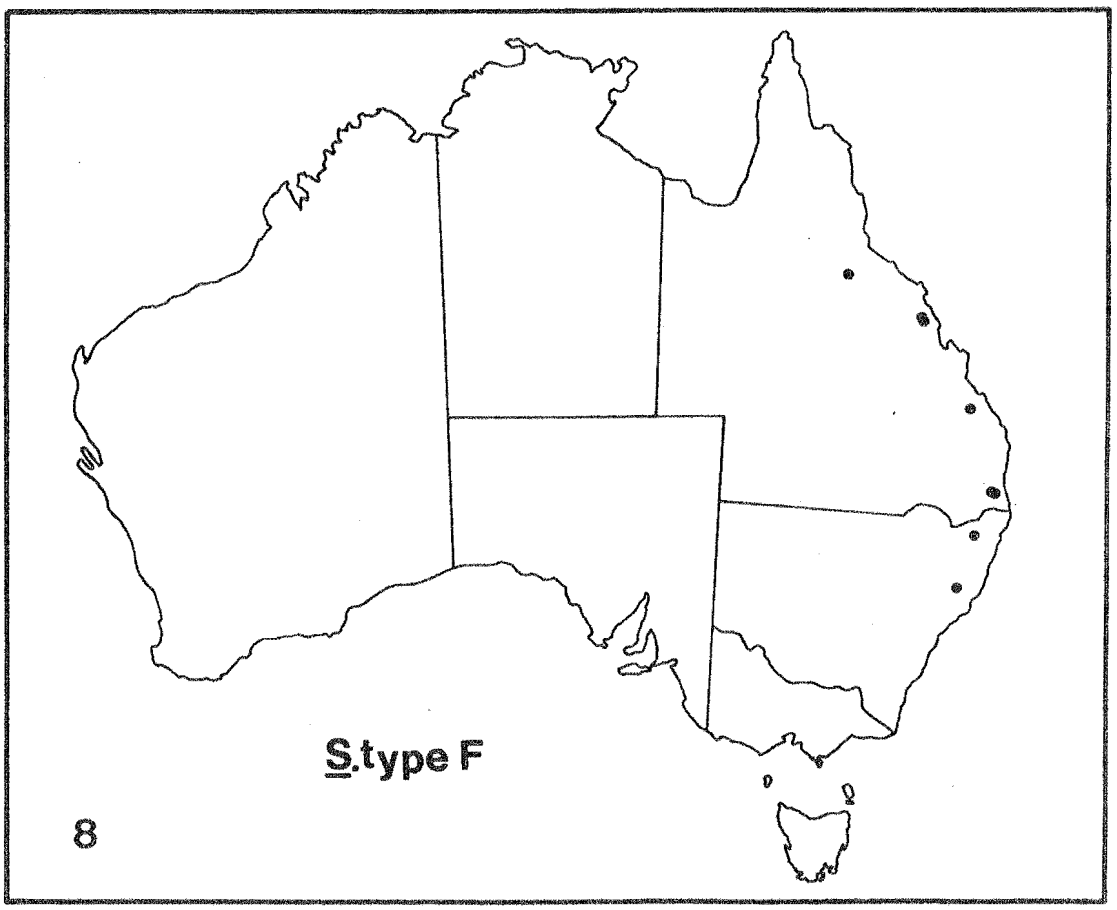


FIGURE 4.20 Records of *Sclerocyphon* type F. Total number of records is shown at lower left.

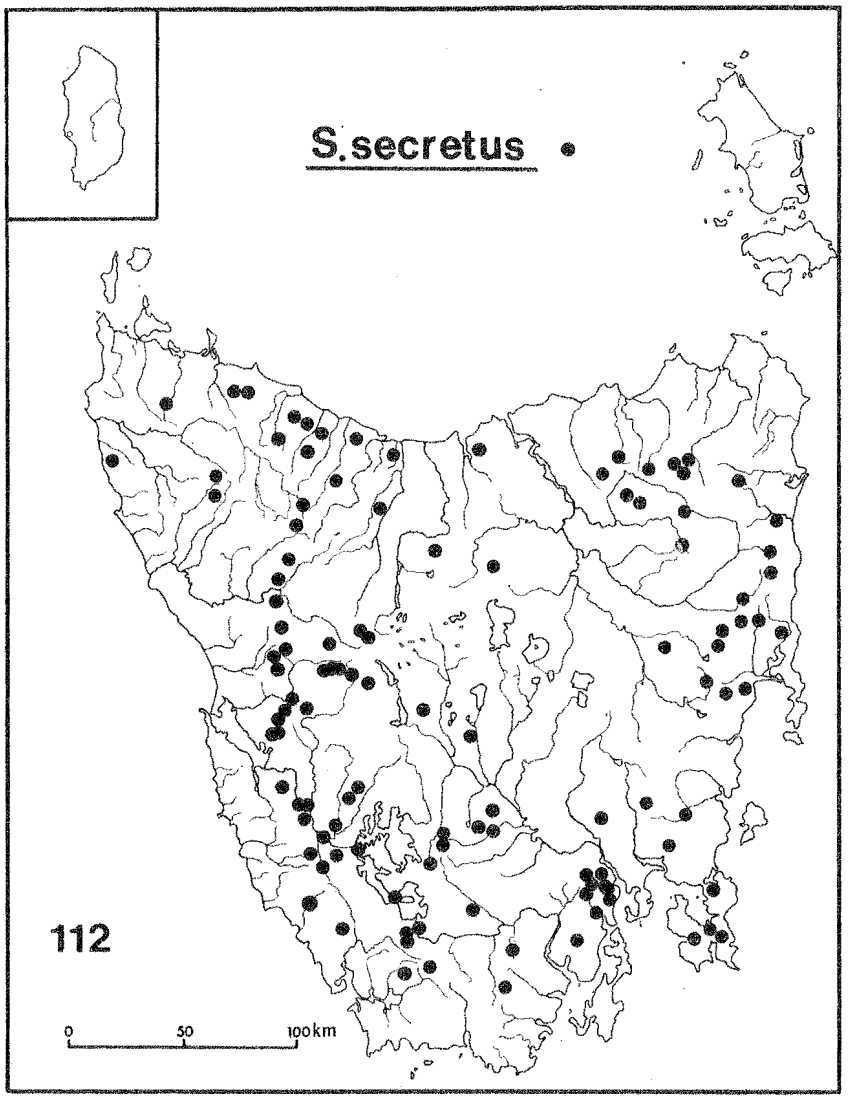


FIGURE 4.21 Distribution of *Sclerocyphon secretus*. Total number of records is shown at lower left.

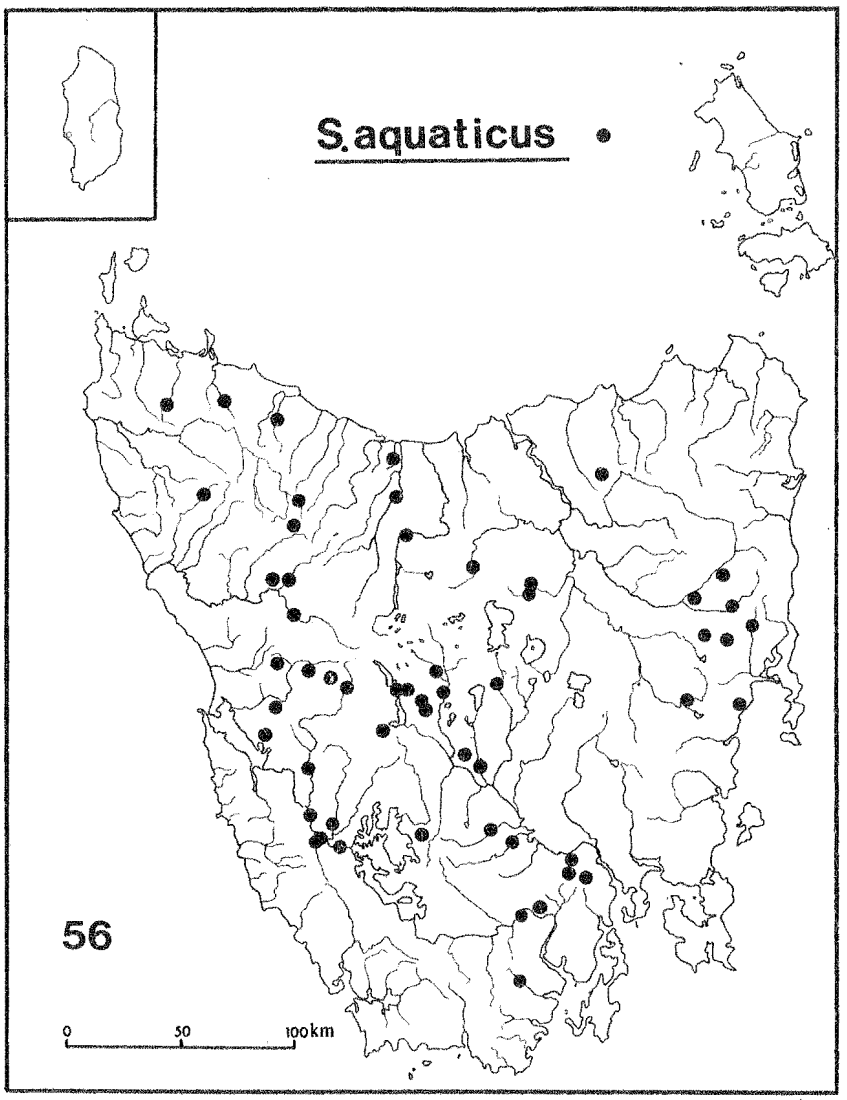


FIGURE 4.22 Distribution of *Sclerocyphon aquaticus*. Total number of records is shown at lower left.

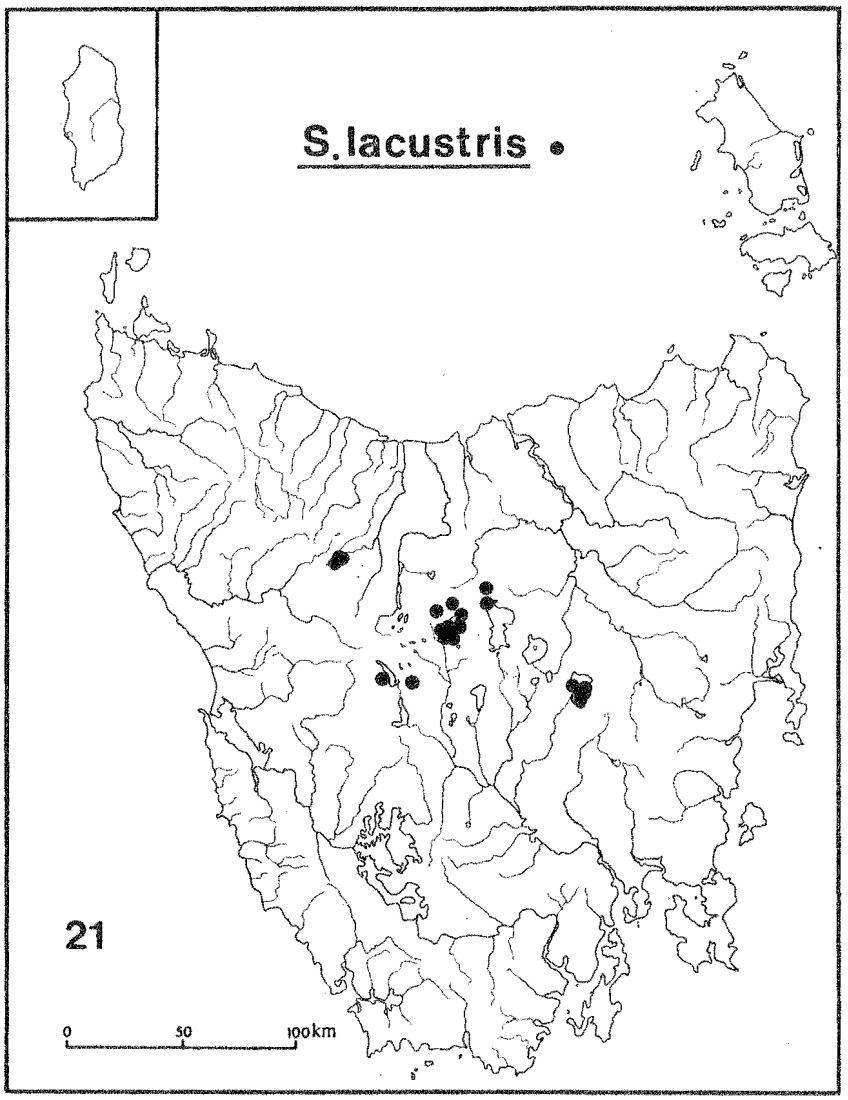


FIGURE 4.23 Distribution of *Sclerocyphon lacustris*. Total number of records is shown at lower left.

Australia has been less comprehensive making it difficult, at present, to discern if the absence of *Sclerocyphon* from a seemingly suitable region is a true one or merely a reflection of a low sampling intensity.

Australian Mainland Species

Sclerocyphon striatus (Figure 4.5)

S. striatus is the most common species of the Australian mainland. It occurs in the rivers and streams of the Great Dividing Range from the region immediately north-east of Melbourne, in Victoria, to the Peel River, on the New England Tableland, in northern New South Wales. This species has also been recorded from the Otway and Grampian Ranges as well as lowland western and eastern coastal regions, in Victoria.

It appears to be most common in that region of the Great Divide known as the Australian Alps (Figure 4.1).

The occurrence of *S. striatus* in both high altitude and lowland habitats indicates that the larvae are tolerant of a fairly wide range of temperature and flow conditions. Adults of this species fly at night as they have been collected at mercury-vapour lamp light traps. This phenomenon has been recorded in only two other species; *S. minimus* and *S. zwicki*.

Sclerocyphon maculatus (Figure 4.6)

This species possesses a distribution similar to, but more restricted than, that of *S. striatus*. It occurs in the rivers and streams of the Great Divide from the region immediately north-east of Melbourne to Dorrigo, on the eastern edge of the New England Tableland, in northern New South Wales. West of Melbourne it has been recorded from the Otway Ranges and Meredith but not from the drier regions further west which are inhabited by *S. striatus* and *S. armstrongi*.

S. maculatus is most abundant in the Victorian section of the

Australian Alps but elsewhere it is far less common than *S. striatus*. Although it displays a predominantly upland distribution its occurrence in several lowland areas, including the Morwell-Traralgon district of south-eastern Victoria, and Sydney (exact locality not specified) indicates that it is not entirely restricted to higher altitudes.

Further collection in New South Wales is needed to determine the northern limits of the distribution of this species.

Sclerocyphon zwicki (Figure 4.7)

This species resembles the previous two in its distribution although its range is considerably more restricted. It occurs along the Great Divide from the YarraRiver, in south-eastern Victoria, to Barrington House, near Salisbury, on the southern edge of the New England Tableland, in New South Wales and appears to be restricted to high altitudes.

Larvae have rarely been collected in large numbers at any site and they appear to be less abundant and to occur in fewer streams than either *S. striatus* or *S. maculatus*. However, the larvae appear to be restricted to rocks in the most torrential sections of large rivers which makes them difficult to collect (Dr. P. Zwick, pers. comm.) and thus possibly so appear even rarer.

The restriction of *S. zwicki* to both larger streams (and rivers) and high altitudes suggests that it requires constant, moderate to fast flow regimes and cool water.

Sclerocyphon basicollis (Figure 4.8)

S. basicollis, which occurs along the east coast of Australia from Melbourne, in south-eastern Victoria, to Kuranda, in northern Queensland, is the most widespread species. Its distribution is virtually continuous along both the Great Divide and the coastal lowlands from Melbourne to

Cooran in southern Queensland. An apparent disjunction occurs between the latter site and northern Queensland. Further collecting is necessary to determine whether this disjunction is a real one or merely a product of insufficient sampling.

Although this species has been recorded from both highland and lowland regions it appears to be more common in lowland streams. This suggests that the species is tolerant of a fairly wide range of stream temperatures and flow regimes.

Sclerocyphon minimus (Figure 4.9)

The range of this species is nearly as extensive as that of *S. basicollis*. It occurs in the eastern coastal region and on the eastern slopes of the Great Divide from Minnamurra Falls, near Kiama, in southern New South Wales, to the McIvor Range, 65 km north of Cooktown, in northern Queensland. Its distribution is predominantly northern, the greatest number of specimens having been collected from the Atherton-Cairns region of northern Queensland.

The present distribution is based only on records of the adult as the larval form is still unknown. Once adult and larva have been associated, permitting the identification of larval material in existing collections, and further collecting is carried out, information on the distribution of this species should increase considerably.*

Sclerocyphon armstrongi (Figure 4.10)

This species appears to be restricted to the south-western region of eastern Australia. It is the only species occurring in South Australia and has been recorded from the Mt. Lofty Range and adjacent lowland areas near Adelaide. It also occurs in the Grampian Ranges and adjacent regions in western Victoria. Its occurrence in the generally

* This note also applies to some of the following species.

low altitude streams of these regions suggests that it has adapted to the fairly harsh environmental conditions existing there during the summer months.

These streams experience elevated temperatures and little or no flow during summer.

Sclerocyphon serratus (Figure 4.11)

S. serratus has been recorded only from the type-locality, Tamworth, on the New England Tableland, in northern New South Wales and few conclusions regarding its range and habitat requirements can be made from this single record. The note* also applies to this species.

Sclerocyphon collaris (Figure 4.12)

This species appears to be restricted to Queensland and, in particular, north Queensland, the greatest number of specimens having been collected in the Cooktown-Cairns region. The note* also applies to this species.

Sclerocyphon aquilonius (Figure 4.13)

This species has been recorded only from Crystal Cascades, near Cairns, which is a permanent stream running off the eastern slopes of the Lamb Range, a section of the Great Dividing Range, in northern Queensland. The note* also applies to this species.

Sclerocyphon nitidus (Figure 4.14)

This species has been recorded from only two localities; Lamington National Park in southern Queensland and just across the New South Wales State boundary, at Whian Whian State Forest. It is possible that this species is restricted to streams running through the dense sub-tropical forest in the coastal ranges of this region. The note* also applies to this species.

Sclerocyphon type A (Figure 4.15)

Larvae of this type appear to be restricted to the Atherton-Cairns region of northern Queensland and, as already suggested (Chapter 3) they may well be the larvae of *S. aquilonuis*, which also appears to be restricted to this region.

Association with its adult and further sampling is needed to accurately determine the range and habitat requirements of this type**.

Sclerocyphon type B (Figure 4.16)

This larval type has a predominantly southern Queensland distribution although it has been recorded from one locality further north, the Alice River at Townsville. Larvae of this type occur in the lowland streams of the coastal region which attain high temperatures during the summer months and they may well have evolved in response to this particular environment. See note**.

Sclerocyphon type C (Figure 4.17)

The range of this larval type is fairly extensive as it occurs from Coen, on Cape York Peninsula, in northern Queensland to the Armidale-Kempsey region, on the eastern slopes of the New England Tableland, in northern New South Wales. Its occurrence in Upper Lanelly Creek, in the Coen district of Cape York Peninsula represents the northern-most record of *Sclerocyphon*.

The distribution of this larval type is predominantly northern, the greatest number of specimens being recorded from the Atherton-Cairns district of northern Queensland. This type may represent the larval form of *S. minimus* (as suggested in Chapter 3) on the basis of their similar distribution. See note**.

** This note applies to all the larval types.

Sclerocyphon type D (Figure 4.18)

This larval type has been recorded from only one locality, Lamington National Park in southern Queensland. This type may represent the larval form of *S. nitidus* (as suggested in Chapter 3) on the basis of their similar distributions. See note**.

Sclerocyphon type E (Figure 4.19)

This larval type has been recorded from only two localities, a creek near Tamworth and a creek at Barrington, at high altitudes on the New England Tableland, in northern New South Wales. This type may represent the larval form of *S. serratus* (as suggested in Chapter 3) on the basis of their similar, restricted, distributions. See note**.

Sclerocyphon type F (Figure 4.20)

This larval type is fairly widespread, its range extends along the east coast from the Burdekin River in northern Queensland to the Armidale-Kempsey region of the eastern slopes of the New England Tableland in northern New South Wales. See note**.

Tasmanian Species

The three species described below are all endemic to Tasmania.

Sclerocyphon secretus (Figure 4.21)

This species is the most common and widespread of the Tasmanian species of *Sclerocyphon*. The larvae occupy a diverse range of habitats, occurring both in large, cold fast-flowing streams and rivers and in much smaller streams of variable flow. Some of these smaller streams experience relatively high temperatures and dry up into pools in the summer. Larvae occur in both lowland and upland streams, but never above the treeline. From Figure 4.21 it can be seen that *S. secretus* occurs in

all regions of Tasmania except the lakes of the Central Plateau and the soft, granite substrates of the north east.

Sclerocyphon aquaticus (Figure 4.22)

This species occurs throughout most of Tasmania but it is far less common than *S. secretus*. It appears to be restricted to the cool, larger streams and rivers of moderate to fast, permanent flow. Substrate plays some part in determining the occurrence of this species. It is most common on dolerite substrates but does not occur on the white quartz substrates that predominate in many of the streams of the west and south-west of Tasmania or on the soft granite substrates of north eastern streams.

Sclerocyphon lacustris (Figure 4.23)

This species appears to be restricted to the wave-swept rocky shores of the lakes of the Central Plateau. Its distribution extends from Dove Lake in the north-west of the Plateau, to Pine Lake in the north-east, Lake Sorell and Lake Crescent in the south-east and Shadow Lake in the south-west of the Plateau.

It is likely that this species is present in most of the lakes of the Central Plateau that are large enough to experience some wave action and have not been affected by hydro-electric power generation developments. A number of lakes on the Central Plateau have had their water levels raised for power generation and these levels are subject to considerable long-term and short-term fluctuations. Although the natural lakes of the Central Plateau also experience considerable fluctuation in level during the course of a year they still possess a well-developed, extensive rocky shore line. It is this lack of an established rocky shore in developed lakes that is probably limiting to the presence of *S. lacustris*.

S. lacustris larvae were present in Great Lake in 1953 (Chapter 3). However, this lake has since been part of a major power development and

its water level has been raised considerably on two separate occasions. *S. lacustris* has not been found in Great Lake during the present study.

4.4 Discussion

Factors Influencing the Distribution of *Sclerocyphon*

Physiography

The distribution of *Sclerocyphon* in Australia is illustrated in Figure 4.24 (compiled from Figures 4.5 - 4.23, the distributions of each species). A comparison of this map with the orographic map (Figure 4.2) reveals that the distribution of the genus is virtually restricted to the Eastern Highlands. With the exception of *S. armstrongi*, which is found in South Australia, all Australian mainland species of *Sclerocyphon* have been recorded from the slopes of the Great Dividing Range or the lesser ranges and coastal plains between the Great Divide and the eastern seaboard.

However, it is not the Eastern Highlands *per se* that control the distribution of the genus but rather the climatic and geological conditions that exist in the region. Keast (1959) noted that the Great Divide is a vast rainfall trap and as such provides a wide range of environments. Consequently it is the scene of much of the biological diversity of the Australian continent.

Climate

Comparison of the distribution map of the genus (Figure 4.24) and the rainfall map of Australia (Figure 4.3) reveals that the majority of Australian mainland *Sclerocyphon* have been recorded from the coastal strip of eastern Australia experiencing more than 750 mm of rain annually. In both Victoria and New South Wales some larvae have been recorded from west of the 750 mm isohyet, in regions receiving as little as 500 mm of rain a year. *Sclerocyphon* occurs throughout Tasmania which receives

FIGURE 4.24 Distribution of *Sclerocyphon* in Australia.

FIGURE 4.25 Faunal provinces in Australia (after Mackerras, 1970).

500-750 mm of rain per annum on the east coast increasing to a maximum of 3660 mm on the west coast.

The widespread distribution of *Sclerocyphon* from Cape York, in the north of Australia, to Tasmania, in the south, indicates that temperature, alone, may not be a limiting factor. However some species appear to possess definite upper limits of thermal tolerance.

The range of climatic zones occupied by species is documented in Table 4.1. This table indicates the occurrence of species in the climatic zones constructed from Thornwaites' (1933) method of classification (see Figure 4.4).

A number of species, including *S. maculatus, S. zwicki, S. nitidus, S. serratus, S. secretus, S. aquaticus, S. lacustris* and larval types D and E, are restricted to regions of low to moderate temperatures and year-round rainfall.

S. basicollis and *S. minimus* both extend over the greatest number of zones (4), indicating that they are able to cope with a greater range of temperatures and winter-deficient rainfall. *S. striatus*, although recorded from a smaller number of zones (3), appears to be the species best adapted to variable rainfall conditions. This species has been recorded in areas experiencing three different rainfall regimes; abundant year-round rainfall, winter-deficient rainfall and summer-deficient rainfall.

A summer-deficient rainfall regime is likely to present an extremely harsh environment to larvae of *Sclerocyphon*. Larvae are dependent upon dissolved oxygen for respiration. During summer when water temperatures are high, the amount of available oxygen decreases and if the flow is also reduced, lack of dissolved oxygen may well become a limiting factor to the species. Although last instar larvae may escape this situation by leaving the water and breathing air through the spiracles until pupation takes place, this option is not available to larvae of earlier instars

TABLE 4.1 Climatic zones occupied by species of *Sclerocyphon*.

Species	Presence in climatic zones						Characteristics of climatic zones occupied		
	AA'r	BA'w	BB'r	CA'w	CB'r	CB's	Humidity	Temperature	Rainfall
S. basicollis	x	x	x		x		wet, humid, sub-humid	tropical, meso-thermal	abundant all seasons, winter deficient
S. minimus	x	x	x		x		wet, humid, sub-humid	tropical, meso-thermal	abundant all seasons, winter deficient
S. striatus			x		x	x	humid, sub-humid	mesothermal	abundant all seasons, winter deficient, summer deficient
S. maculatus			x		x		humid, sub-humid	mesothermal	abundant all seasons
S. zwicki			x		x		humid, sub-humid	mesothermal	abundant all seasons
S. armstrongi					x	x	sub-humid	mesothermal	abundant all seasons, summer deficient
S. collaris		x					humid	tropical	winter deficient
S. aquilonius	x						wet	tropical	abundant all seasons
S. nitidus					x		sub-humid	mesothermal	abundant all seasons
S. aquaticus			x				humid	mesothermal	abundant all seasons

S. secretus			x		humid	mesothermal	abundant all seasons
S. lacustris			x		humid	mesothermal	abundant all seasons
S. type A	x				wet	tropical	abundant all seasons
S. type B		x		x	humid, sub-humid	tropical meso-thermal	abundant all seasons, winter deficient
S. type C	x	x		x	wet, humid, sub-humid	tropical, meso-thermal	abundant all seasons, winter deficient
S. type D				x	sub-humid	mesothermal	abundant all seasons
S. type E			x		humid	mesothermal	abundant all seasons
S. type F		x	x	x	humid, sub-humid	tropical, meso-thermal	abundant all seasons, winter deficient

(since only last instar larvae possess functional spiracles).

S. armstrongi is the only other species known to occur in a summer-deficient rainfall zone. This species may have evolved in response to this particular type of climate as it appears to be virtually restricted to this zone (Table 4.1). *S. secretus* larvae have been collected from streams on the east coast of Tasmania which experience periods of little or no flow and elevated temperatures; however these conditions do not prevail for as long as they do in regions of the Australian mainland.

Only a small number of species on the Australian mainland have been recorded from a single climatic zone: *S. aquilonius* and *S* type A (which are possibly synonymous), *S. nitidus* and *S.* type D (possibly synonymous) and *S. serratus* and *S.* type E (possibly synonymous). *S. aquilonius* and *S.* type A are of particular interest as they appear to be restricted to the unique wet tropical region of the Atherton-Cairns district of northern Queensland. As noted previously (Chapter 3), on the basis of morphology *S* type A appears to be the most primitive larval form in Australia. These larvae may in fact be a relict population of a species that existed in Australia when wet tropical conditions were considerably more widespread than they are today, that is, during the early Tertiary.

This ancestral species probably occurred much more widely under such conditions and it is likely that climatic changes since the Tertiary have caused its range to contract until it is now found only in the Atherton-Cairns region.

The apparent absence of *Sclerocyphon* from seemingly suitable climatic zones in the north of the Northern Territory and the south-west of Western Australia is still to be confirmed. The northern region of the Northern Territory has not been sampled specifically for *Sclerocyphon* and future collecting there may reveal its presence. Some collecting has been carried out in the south-west of Western Australia and the absence of

Sclerocyphon there may be explained by two factors. The summer-deficient rainfall regime appears to be harsher than that experienced in the south-east of Australia and therefore may be limiting to *Sclerocyphon*. The substrate of most streams sampled was granite and the soft, quickly-eroding surfaces appear to be unsuitable for colonisation by *Sclerocyphon* larvae. As noted in the previous section, *Sclerocyphon* larvae are absent from the granitic substrates of streams and rivers in the north-east of Tasmania.

Habitat

The most important factor determining the occurrence of *Sclerocyphon* within a suitable climatic zone appears to be the presence of suitable substrates. The habitat of psephenid larvae in the United States has been described as clear streams of moderate to rapid flow with gravelly or rocky bottoms (Leech and Chandler, 1956). The habitats of most *Sclerocyphon* in Australia appear to be similar although rocky rather than gravelly substrates are preferred. Field observations suggest that the ideal substrate is provided in streams where rocks are neither too mobile nor so firmly cemented into the substrate matrix that larvae cannot move down into the rock-mud interface.

As larvae remain adpressed to rock surfaces throughout life it is reasonable to suggest that the actual surface quality of the rocks will play some part in determining the occurrence of larvae. In Tasmania the greatest number of larvae have been collected from dolerite substrates.

Sclerocyphon larvae are usually absent from streams in which significant algal growth is present. Such growth often occurs in streams running through agricultural areas, as a result of nutrient enrichment. The presence of such algal growth greatly restricts the area available to larvae for locomotion and grazing.

Larvae are rarely found in streams where the surrounding vegetation has been removed or is naturally absent. Such streams include those running through cleared farming land and also high-altitude streams above the treeline. The removal, or lack, of riparian vegetation results in considerable fluctuations in stream temperatures and probably much warmer streams overall. This vegetation is also a necessary feature of the adult habitat. The presence of suitable riparian vegetation is probably another factor contributing to the observed correlation of the distribution of *Sclerocyphon* with the Eastern Highlands as Keast (1959) notes that all of the rainforests and most of the sclerophyll forests of the Australian mainland occur between the Great Divide and the eastern coastline.

Zoogeographical Regions

Australia has been divided into a number of zoogeographical regions on the basis of faunal and ecological characteristics. The most widely accepted provinces are those of Spencer (1896) who divided the continent into the Bassian, Torresian and Eyrean faunal provinces. Mackerras (1970) modified the original Bassian province, extending it in a northern tongue along the higher parts of the Great Dividing Range. These faunal provinces, as modified by Mackerras (1970), are illustrated in Figure 4.25.

The following nine species and one larval type are totally Bassian; *S. aquaticus*, *S. secretus*, *S. lacustris*, *S. armstrongi*, *S. striatus*, *S. maculatus*, *S. zwicki*, *S. serratus* and *S.* type E. Three species and three larval types are totally Torresian; *S. aquilonius*, *S. collaris*, *S. nitidus*, *S.* type A, *S.* type B and *S.* type D. *S. basicollis*, *S. minimus*, *S.* type C and *S.* type F occur in both the Bassian and Torresian provinces.

The preponderance of species in the Bassian region suggests a southern, Gondwanaland, origin of the genus. Alternatively, it may be argued that the Bassian region merely provides a greater number and

diversity of suitable habitats for *Sclerocyphon* at the present time. The possible Gondwanaland origin of the genus is discussed further in the following section.

Some Comments on the Historical Biogeography of *Sclerocyphon*

The Tasmanian species of *Sclerocyphon*

Mackerras (1970) suggests that in a zoogeographical study a researcher must look for barriers that may have separated discrete populations long enough to permit the evolution of reproductive isolation. One such barrier is immediately obvious when considering the Tasmanian species of *Sclerocyphon*; that of Bass Strait.

The three species recorded from Tasmania, *S. aquaticus*, *S. secretus* and *S. lacustris*, are endemic and no species of the Australian mainland have been recorded in Tasmania. This complete endemism suggests that the Tasmanian and Australian mainland species have been separated for a considerable period of time, long enough for the separate species to evolve from an ancestral species common to both regions (as proposed by the phylogenetic classification given in Chapter 3).

High levels of endemism are present in many of the groups of invertebrates that have been thoroughly studied on both sides of Bass Strait. Zwick (1977a) noted the occurrence of six species of Blephariceridae in Tasmania, all of which appear to be endemic. The Blephariceridae resemble the Psephenidae fairly closely in the ecological requirements of the larvae. Endemism levels of 82-84% occur in the Tasmanian Plecoptera (Hynes and Hynes, 1980) and 74% in the Trichoptera (Neboiss, 1977). Hynes and Hynes (1980) suggest that the high level of endemism in the Plecoptera can be explained by the inhospitable conditions existing in the Bass Strait region when, as a result of lowered sea levels during the Pleistocene, it was open. This explanation may well also account for the complete endemism

of Tasmanian *Sclerocyphon*.

Friend (1980), working on Tasmanian terrestrial amphipods, examined the levels of endemism in a number of well-studied groups, in particular terrestrial and inland aquatic invertebrates, and demonstrated that a fairly close inverse relationship exists between levels of endemism and species' vagility. The vagility of *Sclerocyphon* species appears to be low. The main dispersal phase of *Sclerocyphon* is the adult. However this dispersal phase is very much restricted as the beetles are short-lived and for much of their life-span display a cryptic mode of behaviour. The beetles mostly remain hidden beneath the litter and debris at the edges of the stream; mating takes place here, then the females return to the water to lay their eggs. Although the beetles are capable of flight the duration of the flight phase appears to be very short and they do not form part of the aerial plankton.

Species probably disperse by "stream-hopping" and thus Bass Strait, either as it is today, or as the arid windswept plain it appears to have been during the Pleistocene (Hynes and Hynes, 1980) has presented an impassable barrier to the genus.

Sclerocyphon has not been recorded from Flinders Island or King Island but as intensive sampling has not been conducted on either island during the present study, it is not known if this absence is a real one. It has been suggested (Hynes and Hynes, 1980) that the Wilson's Promontory-Flinders Island route would have been a poor one for stoneflies as these regions and the nearby north-eastern Tasmanian mainland are composed of a coarse-grained granite which weathers quickly to a rough sand, resulting in little formation of stony riffles. Similarly this route would also have been a difficult one for *Sclerocyphon*. As already stated, no larvae have been recorded from the granitic substrates of the north-east. This is probably due to both the lack of stony riffles and the soft sandy rocks that are present, providing a poor surface for larvae to cling to

or graze on. Whether the King Island region provided a suitable bridge for *Sclerocyphon* during the Pleistocene will not be known until the presence or absence of the genus on the island is verified.

The low vagility of *Sclerocyphon*, as discussed above, together with information from the phylogenetic classification of the genus (Chapter 3) indicating that the Tasmanian species are descendants of an ancestral species common to both Tasmanian and the Australian mainland, suggests that the presence of the genus in Tasmania may be best explained by vicariance. The first flooding of Bass Strait during the Miocene probably fragmented the range of the ancestral species by effectively isolating it's Tasmanian members. Bass Strait appears to have remained a barrier to species dispersal even during subsequent openings (as discussed above) and subsequent changes in the Tasmanian environment, in particular the dramatic climatic changes of the Pleistocene, influenced the speciation of the ancestral species (as outlined in Chapter 3) resulting in the presence of the three endemic species in Tasmania today.

The Australian Mainland Species of *Sclerocyphon*

It is probable that the distribution of *Sclerocyphon* was more widespread in Australia during the early Tertiary, a period when wet tropical conditions were considerably more widespread than they are today. Evidence of this is provided by the most primitive larval type, *S.* type A, (Chapter 3) which, as noted in a preceding section, is presently restricted to the Atherton-Cairns district of northern Queensland, but is probably a relict population of a species that was once more widespread.

S. zwicki and *S. aquaticus*, which on the basis of larval characters are also considered to be primitive (Chapter 3), although more advanced than *S.*type A, are presently restricted to cool, permanent rivers and streams. This suggests that they are descendants of species that evolved during the onset of cooler times in Australia, towards the end of the Miocene. This also suggests that all other species, which on the basis of

larval characters are more advanced than the three discussed above, are descendants of species that could only have arisen since the late Tertiary.

Mayr (1963) states that

> "...geographic speciation is the almost exclusive mode of speciation among animals."

and it is likely that species of the *S. maculatus* and *S. striatus* species-groups (Chapter 3) have evolved in response to environmental changes that have occurred in Australia from the Pleistocene to the Recent. Galloway and Kemp (1981) suggest that the vicissitudes of this period, the Quaternary, were extremely rapid in geological terms and imposed severe stresses on life forms. They also suggest that

> "...the present distribution of plants and animals in Australia is a very recent - and temporary - phenomenon."

Although the phylogenetic classification of *Sclerocyphon* proposed in Chapter 3 provides a basis for the zoogeographical study of the genus this study is considerably hampered by the lack of data on the distributions of many of the Australian mainland species. More data must be obtained for any further conclusions to be drawn.

The Possible Gondwanaland Origin of *Sclerocyphon*

As previously noted (Chapter 3) *Sclerocyphon* (or a very closely related genus) occurs in Chile, as well as Australia, but nowhere else in the world. This disjunct southern distribution in a genus with apparently low vagility, as demonstrated in the previous discussion on the endemism of the Tasmanian species, seems to be best explained by the vicariance model of historical biogeography. This suggests that the

progenitor of *Sclerocyphon* would have been present in Gondwanaland before the separation of the Australian plate, 55 m.y. ago. The rifting of Australia and later South America from the original Gondwanaland plate, as proposed by the theory of continental drift (or plate tectonics), fragmented the range of this ancestral species and created the disjunction evident today.

Hedley (1912 cited by Brundin, 1966) proposes that dispersal between Australia and South America was only a one way process with Australia being the recipient of South American species. If this was so then it must be postulated that the progenitor of *Sclerocyphon* arose in South America. No *Sclerocyphon* (or any other psephenid species) have been recorded from New Zealand suggesting that *Sclerocyphon* reached Australia after New Zealand had separated from Gondwanaland, 80 m.y. ago. However, this apparent absence of the genus from New Zealand must still be verified.

Darlington (1963) put forward an elaborate hypothesis of southern distributions based on radiation from the Old World tropics. However Raven and Axelrod (1972) suggest that Ockham's Razor must rule out this scheme.

Winterbourn (1980), in a review of the affinities and zoogeography of the aquatic insect faunas of Australia and New Zealand, notes that a number of freshwater insect groups appear to be derived from an old Gondwanaland fauna whose vicariance is a result of continental drift since the Cretaceous. These include the plecopteran families Eustheniidae, Austroperlidae, Notonemouridae and Gripopterygidae (Illies, 1965), although Zwick (1979) suggests different origins for the Eustheninae and Stenoperlinae, subfamilies of the Eustheniidae. The ephemeropteran families, Leptophlebiidae (Edmunds, 1972) and Siphlonuridae (Edmunds, 1972 and Penniket, 1961) and the trichopteran families, Hydrobiosinae, Kokiriidae, Oeconesidae, Tasmiidae, Calocidae, Helicophidae, Conoesucidae and Philorheithridae (Neboiss, 1977) also possesses present-day dis-

tributions which suggest Gondwanaland origins. In the Chironomidae, Brundin (1966) considered that the distribution patterns of the Podonominae, Aphroteniinae and some Diamesinae were evidence of their southern origin.

Main (1981) notes that many beetle families are Mesozoic (principally Jurassic) in origin and the most common older element affinities of Australian beetles are with South America. The taxonomy and relationships of Australian aquatic beetles (those with larval or adult aquatic stages) are poorly known (Winterbourn, 1980) except for two recent studies by Zwick (1977b) on *Hydraena* (Hydraenidae) and Watts (1978) on the Dytiscidae. Zwick (1977b) suggests that the Australian species of *Hydraena* are recent arrivals from the Orient. Watts (1978) found a high specific endemicity in the southern Bassian region, and a low generic endemicity in the Torresian and Eyrean regions, in the Australian Dytiscidae.

A number of freshwater insect groups also show northern affinities and Winterbourn (1980) suggests that these may represent more recent elements in the Australasian fauna. The Eubrianacinae, Psephenoidinae and Eubriinae have all been recorded from Indonesia (following section) but no species appear to have reached Australia from the north. The eubriine genera recorded from Indonesia (Bertrand, 1972) appear to be only distantly related to *Sclerocyphon*. No Psephenidae have been recorded from New Guinea; however, an extensive sampling of this island is needed before this absence can be verified.

The reason as to why *Sclerocyphon* is the only genus of the Eubriinae in Australia while elsewhere, for example, in North America, a number of genera occur, is not yet known. It is possible that the progenitor of *Sclerocyphon* was the only psephenid to reach Australia before it separated from Gondwanaland. Alternatively, other genera and other subfamilies may have been present but have since become extinct, resulting in *Sclerocyphon* now filling all stream niches that elsewhere in the

world may be divided between different genera and two or three subfamilies. Unfortunately, unless a fossil history of the Psephenidae in Australia is discovered this question may never be fully answered.

World-wide Distribution of the Psephenidae

The distributions of the Psepheninae (after Brown, 1976; Bertrand, 1972; Murvosh, 1971 and Champion, 1921) the Eubrianacinae, (after Brown, 1976), the Psephenoidinae (after Bertrand, 1972) and the Eubriinae (after Brown, 1980; Bertrand, 1972; Artigas, 1963 and present study) are illustrated in Figures 4.26 - 4.29, respectively. The presence of the four subfamilies in the different zoogeographical regions of the world (Cox *et al.*, 1976) is documented in Table 4.2 and the presence of eubriine genera in these regions is given in Table 4.3.

Hinton (1966) suggests that the world-wide distribution of the family indicates a pre-Eocene origin and similarly the world-wide distribution of the Eubriinae suggests a pre-Eocene origin of genera within this subfamily. Fossil records do not negate this suggestion as a fossil *Eubrianax* larva has been recorded from middle Eocene deposits in France (Bertrand, 1963) while the fossil *Psephenus lutulentus* has been recorded from the Florissant (Oligocene) of Colorado, U.S.A. (Murvosh, 1971).

Apart from Hinton's (1966) work, no other theory as to the origin and distribution of the Psephenidae has been proposed. This is undoubtedly a consequence of the sparse information available on both the distribution and systematics of many psephenid species. The necessity of basing zoogeographical studies on strictly phylogenetic classifications has already been emphasised (Section 4.1), and as the phylogeny of the Psephenidae is still under debate (Chapter 3) conclusions on the origins and directions of dispersal of the Psephenidae are difficult to achieve. Brown (1976) has provided a fairly comprehensive documentation of the

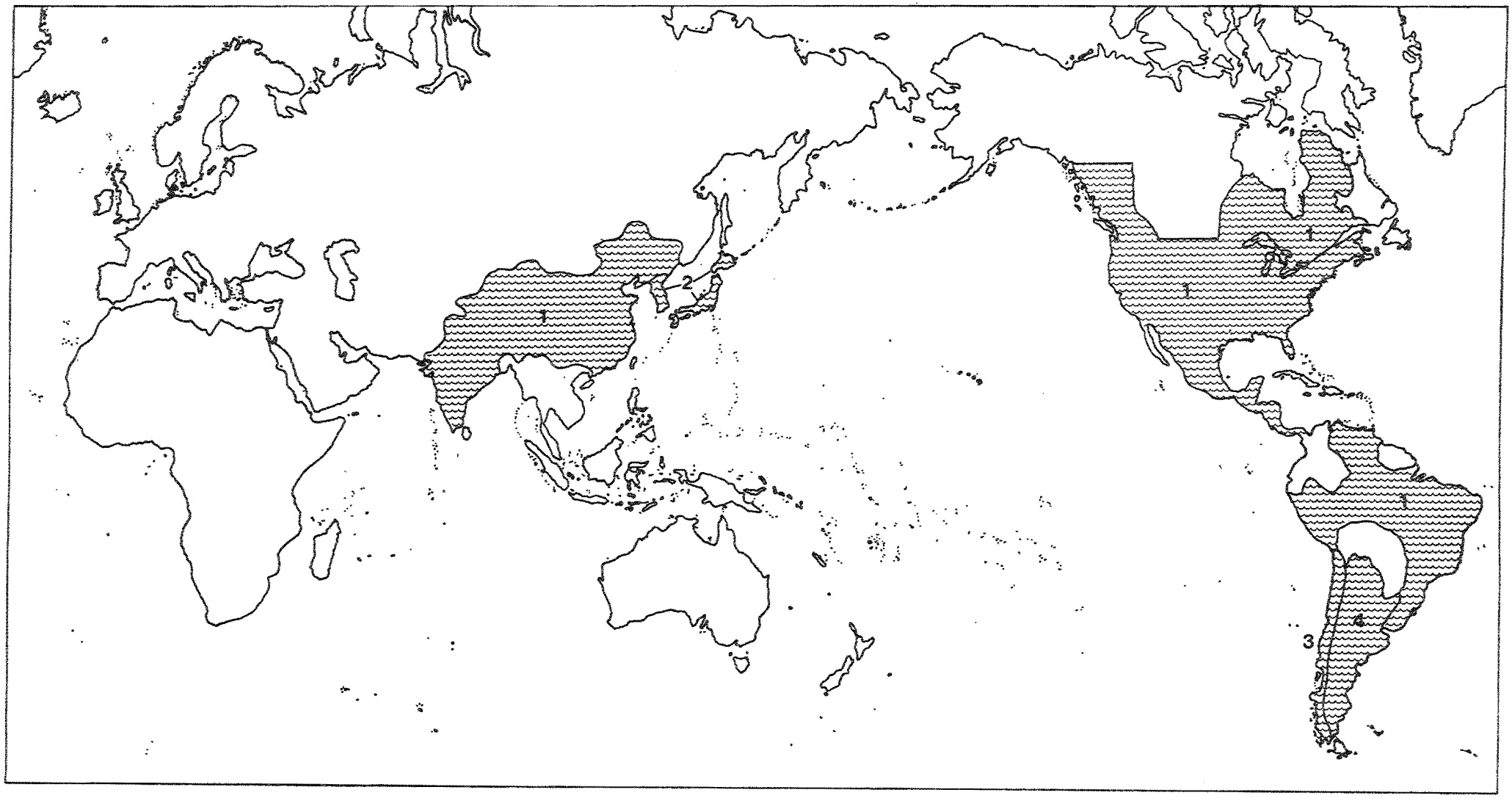


FIGURE 4.26 World distribution of the Psepheninae (after Champion, 1921; Murvosh, 1971; Bertrand, 1972; and Brown, 1976) 1, *Psephenus*; 2, *Mataeopsephenus*; 3, *Tychespsephenus*; 4, *Psephenops*.

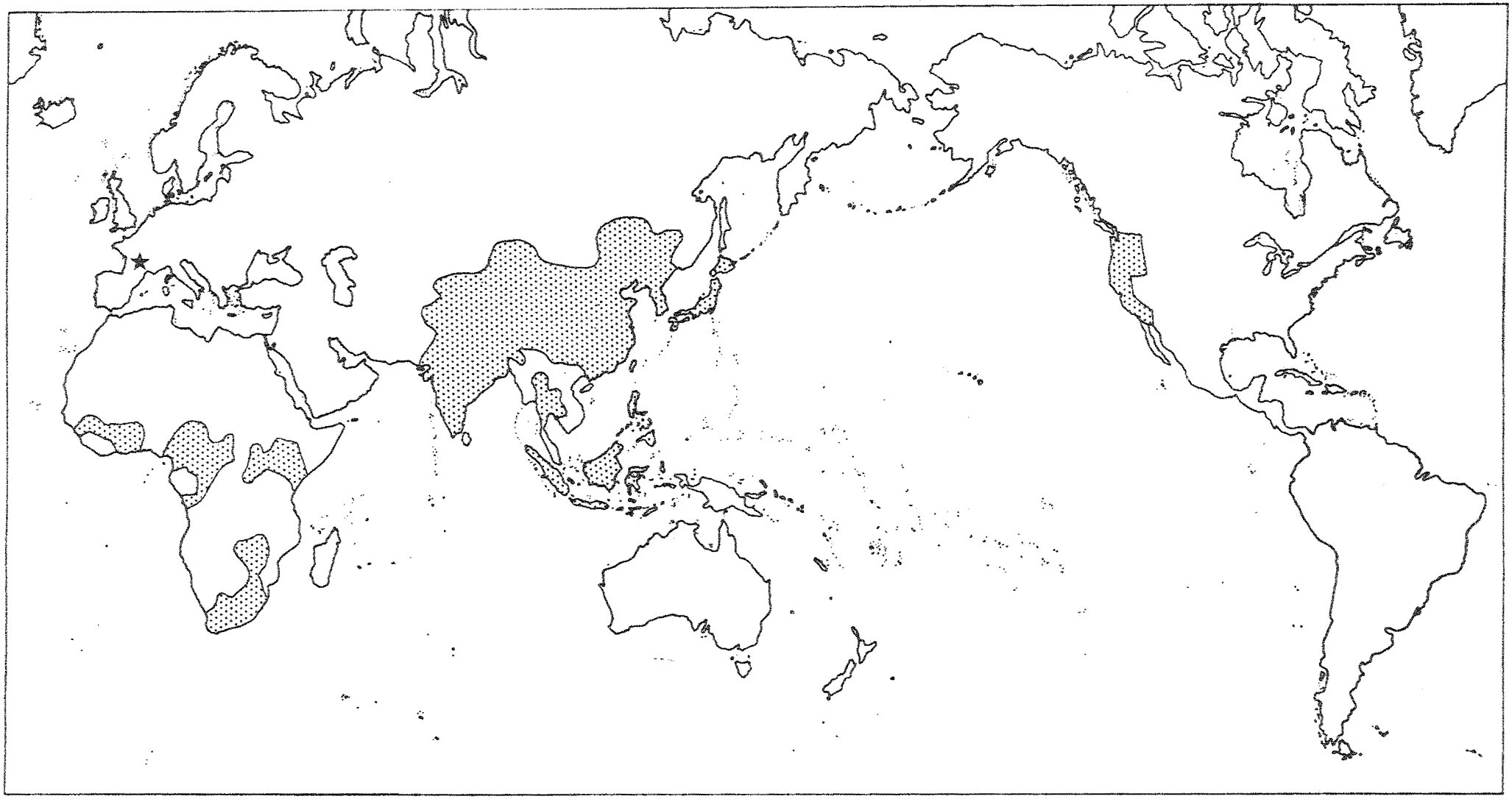


FIGURE 4.27 World distribution of the Eubrianacinae, comprising one genus, *Eubrianax* (after Bertrand, 1964, 1972; and Brown, 1976). Location of the fossil *Eubrianax* marked by a star.

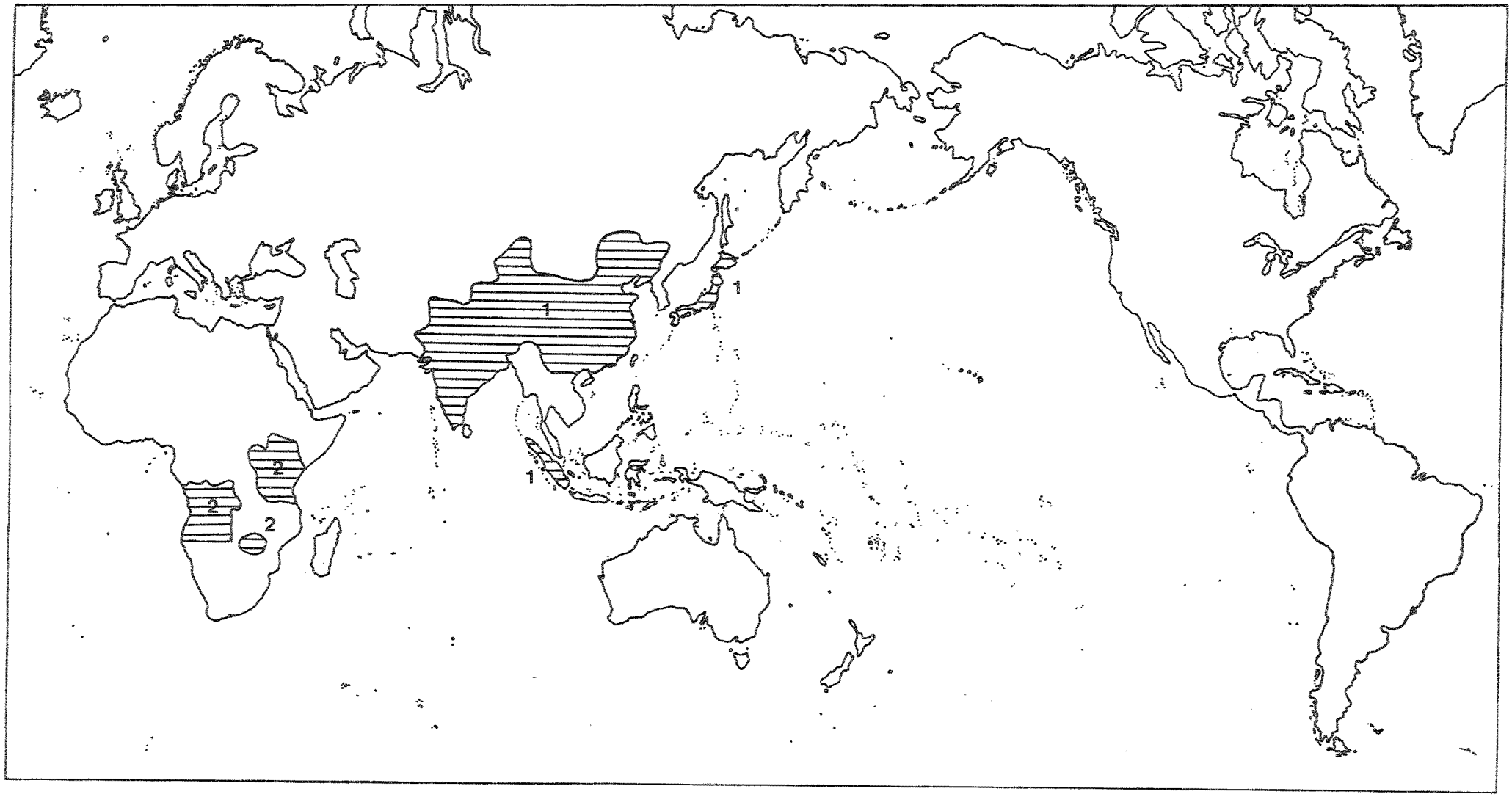


FIGURE 4.28 World distribution of the Psephenoidinae (after Bertrand, 1972). 1, *Psephenoides*; 2, *Afropsephenoides*.

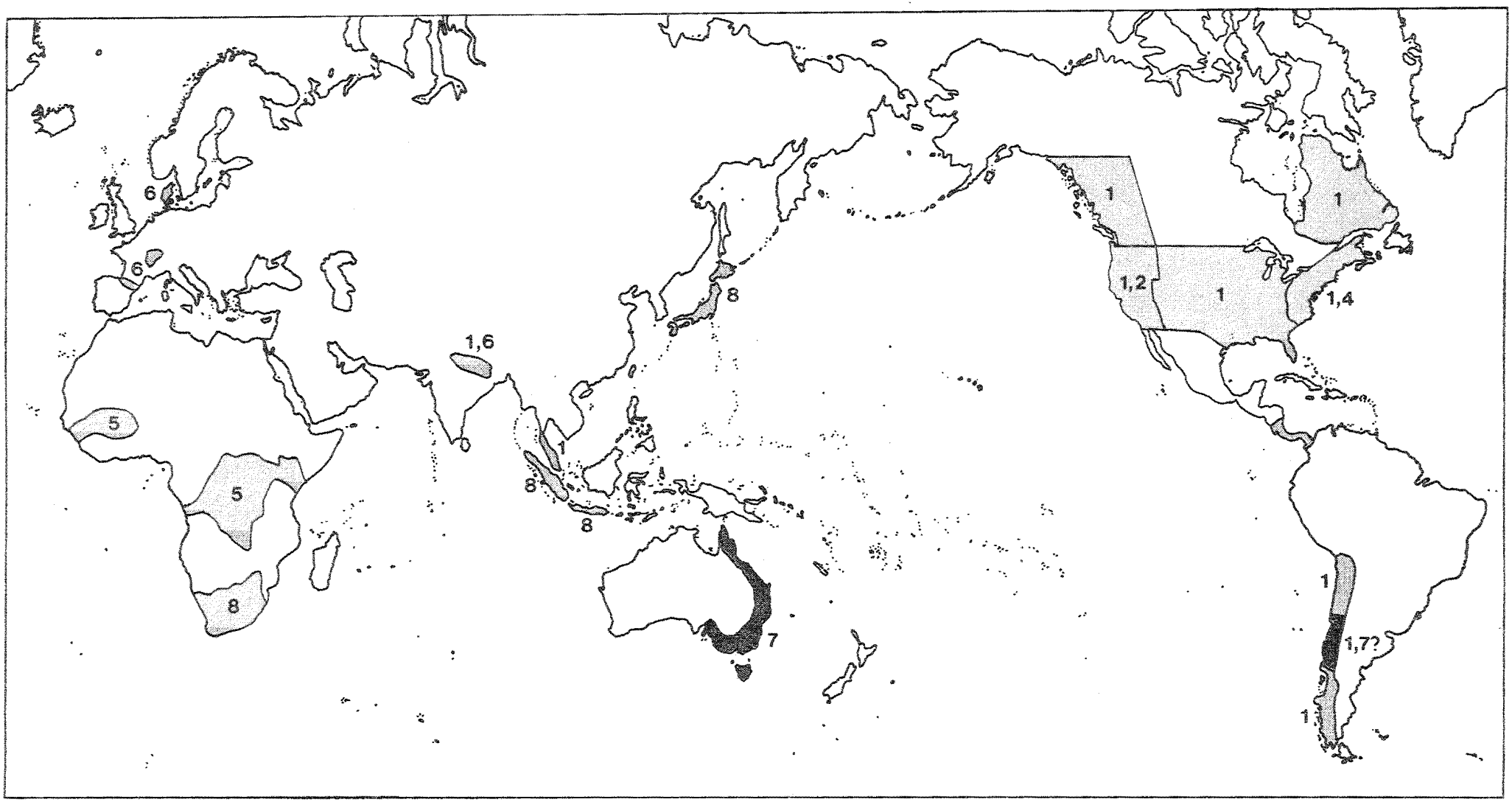


FIGURE 4.29 World distribution of the Eubriinae (after Artigas, 1963; Bertrand, 1972; Brown, 1976, 1980; and present study). 1, *Ectopria*; 2, *Acneus*; 3, *Alabameubria*; 4, *Dicranoselaphus*; 5, *Afroeubria*; 6, *Eubria*; 7, *Sclerocyphon* (darker shading); 8, un-named Eubrinne genera.

TABLE 4.2 Distribution of the psephenid subfamilies in world zoogeographical regions.

Psephenid subfamilies	Zoogeographical regions (after Cox *et al.*, 1976)					
	Nearctic	Palearctic	Oriental	African	Neotropical	Australian
Psepheninae	×	×	×		×	
Eubrianacinae	×	×	×	×		
Psephenoidinae		×	×	×		
Eubriinae	×	×	×	×	×	×

TABLE 4.3 Distribution of the eubriine genera in world zoogeographical regions.

Eubriine genera	Zoogeographical regions (after Cox *et al.*, 1976)					
	Nearctic	Palearctic	Oriental	African	Neotropical	Australian
Ectopria	×		×		×	
Acneus	×					
Alabameubria	×					
Dicranoselaphus	×				×	
Afroeubria				×		
Eubria		×	×			
Sclerocyphon						×
* Eubriide genus type 1			×			
* Eubriide genus type 2			×			
** Eubriide genus 1				×		
*** Eubriide genus 2				×		
*** Eubriide genus (Japan)		×				

* Bertrand (1956, 1972)

** Bertrand (1961, 1972)

*** Bertrand (1972)

three psephenid subfamilies occurring in the United States and the present study documents the distribution of the one genus present in Australia but elsewhere in the world records of psephenid species are often restricted to only one site.

As noted in the previous section, *Sclerocyphon* exhibits low vagility and this appears to be a characteristic of the entire family. Dispersal of the Psephenidae without land connections is therefore difficult to envisage and suggests that a vicariance model may be the best explanation of the current distribution of the family. It seems likely that the origin of the Psephenidae must be traced back to the time when the two supercontinents, Gondwanaland and Laurasia, were united forming a single land mass, Pangaea, in the Jurassic.

Hinton (1966) states that on the basis of reduction in functional respiratory structures all psephenid subfamilies can be derived from the Psepheninae (Chapter 3). Therefore, if the origin and direction of dispersal of the Psepheninae, the most primitive subfamily, is determined, the centre of origin of the entire family will also be known.

Unfortunately the origins and dispersal routes of the Psepheninae, and its apparent sister group, the Eubrianacinae, are not easily determined from an examination of present distribution patterns (Figures 4.26 and 4.27). The occurrence of the fossil *Eubrianax* (Bertrand, 1963) in France indicates a more widespread distribution of this genus in the past as no living representatives exist in France today. It is likely that the Psephenidae were more widespread in the Tertiary when moister, warmer and more constant climatic conditions existed over most of the world. Distributions are likely to have become restricted since the onset of the Pleistocene with its dramatic climatic changes. The origin of the Psepheninae and thus the entire family is a problem that still remains to be solved.

As a result of the present study a hypothesis for the origin and

evolution of the Eubriinae can be proposed.

Sclerocyphon, with the possession of only two gill tufts, rather than three, may be considered the most primitive eubriine genus (Chapter 3) and the disjunct southern distribution of *Sclerocyphon* (or *Sclerocyphon* and its as yet un-named sister group) in Australia and Chile may be considered evidence of a Gondwanaland origin of the genus. From this information it can be suggested that a Gondwanaland origin of *Sclerocyphon* implies a Gondwanaland origin of the entire subfamily.

Within the Psephenidae only the Eubriinae (Figure 4.29) display a world-wide distribution; the Psepheninae, Eubrianacinae and Psephenoidinae each being absent from one or more zoogeographical regions (Table 4.2). The speciation and radiation that has occurred within the Eubriinae (Table 4.3) may well be a consequence of the development of anal retractable gill tufts. The active ventilation of these gill tufts has allowed larvae to colonise habitats with variable levels of dissolved oxygen produced by variable flow and temperature regimes. Such habitats are likely to have become widespread during the Pleistocene.

The Psephenoidinae, the probable sister group of the Eubriinae, possesses a present-day distribution that can also be traced back to a Gondwanaland origin. The members of this subfamily in Africa, India and Asia (Figure 4.28) have most probably evolved from a Gondwanaland progenitor present in Africa and India before the rifting of these areas. Dispersal into Asia probably occurred after India had drifted to its present position, abutting the Asian landmass.

As both the Eubriinae and the Psephenoidinae are considered (in this study) to be derived from the Psepheninae, the postulation of a Gondwanaland origin of these two groups also implies that the psephenine progenitor was present in Gondwanaland prior to the onset of separation. The present distribution of the Psepheninae in South America and India (Figure 4.26) supports this suggestion. However, whether the progenitor

of the Psepheninae first arose in Gondwanaland or reached Gondwanaland from Laurasia still remains to be determined.

CHAPTER FIVE

DESCRIPTION AND ANALYSIS OF LARVAL SHAPE IN THE TASMANIAN PSEPHENIDAE

5.1 Introduction

Examination of a large number of larvae during the taxonomic study of *Sclerocyphon* (Chapter 3) revealed the presence of considerable variation in the shape of the dorsal shield. Differences were evident both within species and between species. An earlier study (Davis, 1975) of larval shape in *Sclerocyphon secretus*, a Tasmanian species, found differences in shape between populations at low and high altitudes in the same stream, Sandy Bay Rivulet, which drains the eastern slopes of Mt. Wellington near Hobart. Initial observations in this study revealed that larval populations of *S. secretus*, the most common species in Tasmania, often differed in shape between different streams. Fewer differences were evident between populations of the other two Tasmanian species, *S. aquaticus* and *S. lacustris*.

The first task of the present study was to find a suitable means of describing the shape of larvae. Once this was achieved the analysis of differences in shape between populations would then be possible. The comparative assessment of shape in living organisms is a complex problem and some of the methods that have been used to characterize and compare biological forms are reviewed by Oxnard (1978). In this study the measurement of lengths and widths at various points across the larval shield was considered the most suitable means of characterizing larval shape. This was largely a consequence of the fact that the description of larval shape was essentially a two-dimensional rather than three-dimensional problem due to the extreme dorso-ventral flattening of the larval shield.

The use of multiple measurements to describe larval shape then dictated the use of multivariate statistical techniques to analyse differences in shape. Such statistical techniques in conjunction with the advent of computer technology are the basis of the fairly new field of multivariate morphometrics. Oxnard (1978) takes care to point out that despite the large amount of morphometric work now being done, the science of morphometrics is still too young and the new methods too little used to know exactly what contribution morphometrics makes to thought in systematics and evolution. He does suggest however that

> "...morphometric methods may well allow large selections of animal forms to tell for themselves, as it were, something of their functional adaptation."
>
> (Oxnard, p.234, 1978)

and it was largely in this spirit that the analysis described below was attempted.

The multivariate method used here was canonical variate analysis. This analysis provides a means of studying interrelationships between pre-determined groups and, in particular, of recognising the distances between groups, while the amount of variability within each group is also taken into account. Each group, in this study, comprised a population of larvae of a single species at a single locality in a stream.

The present study was limited to the Tasmanian *Sclerocyphon* and aimed at obtaining answers to the following questions.

1. what range of larval shapes exists within each of the three Tasmanian species; *S. secretus, S. aquaticus* and *S. lacustris*?

2. how does the shape of larvae vary between the three species? and

3. what influence may various environmental factors have on the expression of larval shield shape?

Experimental as well as statistical techniques are required to obtain an answer to this last question. As statistical methods alone were used a complete answer cannot be expected here.

5.2 Canonical Variate Analysis

The mathematical procedures involved in the construction of canonical variables and the processes of canonical variate analysis are described by Seal (1966) and Blackith and Reyment (1971).

The technique of analysis of variance is well established as a method for comparison of two or more groups to assess whether there are differences in average response for a single variable between the groups. Canonical variate analysis serves a similar function when the comparison of groups is based on a set of variables rather than a single variable. The need to use a set of variables commonly arises when the quantity on which the comparison is to be based is not directly measurable. In the present study "shape" is such a quantity and measurements of length and width were used to describe larval "shape".

Canonical variate analysis examines variables simultaneously, rather than separately, and takes into account in the process the interrelationships between the variables. Canonical variate analysis involves the transformation of measured variables into a new set of variables, the "canonical variables" which are simply linear combinations of the former. The canonical variables are formed such that the first canonical variable gives the maximum possible separation of groups, the second canonical variable gives the next greatest separation of groups and third and subsequent variables are constructed similarly. The canonical variables are formed under the condition that there is no duplication of information within each one with respect to the separation of the groups.

A necessary condition for the use of canonical variate analysis is that variables are normally distributed. In the present study this

condition was met by using log variables. Logarithmic transformation of the variables ensured that the distribution of variables adequately approximated normal distributions.

If the first two canonical variables explain a high proportion of the observed variation it is possible to give a fairly undistorted representation of the relative positions of the groups in a two dimensional graph based on these first two canonical variables. It must be remembered however, that with such graphs the points plotted are estimates of the mean positions of groups rather than true positions.

It is also sometimes of value to examine the relationships between the canonical variables and the measured variables. By examining the standardized coefficients of the equations which relate the measured variables to the canonical variables (the eigen vectors) it is possible to establish which measured variables are playing an important role in the formation of the canonical variables and so possibly give a biological meaning to the canonical variables.

The "distance" between groups can be conceived as the extent of overlap between groups or the likelihood of misclassification of a member of one group into another. The distance between groups, based on this probablistic interpretation, is known as the Mahalanobis distance. Mahalanobis distance (M-distance) or as it is also known, the generalized statistical distance, D^2, provides a numerical measure of the distance between two groups in the total variable space (in this study: three dimensions) while the canonical variate analysis provides a visual measure of the distance between groups along the axes of maximum group dispersion (Phillips *et al.*, 1973).

Blackith and Reyment (1971) describe the mathematical procedure involved in the computation of Mahalanobis distances. The computation of Mahalanobis distances permits assessment of the acceptability of the hypothesis that two groups are indistinguishable on the basis of measured characteristics.

If the M-distance between any two groups exceeds

$$\sqrt{\chi^2\ (P,\ 0.01)\ (\frac{2}{n})}$$

where P = number of variables used in the analysis

χ^2 (P, 0.01) = tabulated chi-squared value for P degrees of freedom and probability 0.01

n = number of observations per group

then a real distinction exists between the two groups.

Mr. Glen McPherson, Mathematics Department, University of Tasmania, was consulted on the use of canonical variate analysis in this study and all analyses were performed on the Burroughs B6700 computer at the University of Tasmania.

Pilot Study

Although the canonical variate analysis appeared to be the most suitable multivariate statistical method for establishing the existence and extent of differences between groups on the basis of larval shape it was first necessary to carry out a preliminary canonical variate analysis on a small amount of data to establish that this was so.

5.3 Materials and Methods

Groups Included in the Pilot Study

As it was suspected that environmental factors may play some part in influencing the expression of larval shape it was desirable to include groups of larvae from the widest possible range of habitats, in Tasmania, in the analysis. Such groups however had to be already present in the material collected for the taxonomic study (Chapter 3). This entire study was based on the taxonomic collection rather than the collection of new samples. Using these two criteria ten groups of *S. secretus*

and five groups of *S. aquaticus*, as listed in Table 5.1, were chosen for inclusion in the preliminary canonical variate analysis.

Number of Larvae per Group

To facilitate comparison of groups the number in each had to be constant. Fifteen larvae per group was the number arbitrarily decided upon for the preliminary analysis. This number was fairly low but it was chosen because it would enable a large number of groups from a wide range of localities to be included in the final analysis. A higher number, even, for example, 30 larvae per group, would have limited the final analysis to a very small number of groups. In some localities four or five man hours were needed to collect even 15 larvae.

The results of the pilot study would provide some indication of whether 15 larvae per group could be considered statistically viable in this study.

The Size of Larvae in Each Group

It was initially hoped to conduct the analysis on last instar larvae only, so eliminating any variations in shape that may have been attributable to age. This was not possible, however, as many samples contained less than 15 larvae of the last instar, often as a result of the fact that larval collections had been made for taxonomic purposes and many of the last instar larvae collected were not preserved but maintained alive in the laboratory for rearing to adulthood. Restricting the analysis to groups containing at least 15 last instar larvae would also have resulted in the omission of a number of localities possessing larvae of distinctly different shapes, in particular those of the south-west of Tasmania. Several of these localities were in extremely rugged country and had previously been reached by helicopter, a facility that was not available during the present study. One locality, Lake

TABLE 5.1 The number and name of locality-groups of *S. secretus* and *S. aquaticus* included in the preliminary analysis of larval shape (pilot study).

Species	Locality Number	Locality Name
	1	Lambert Creek
	2	Waterworks Creek
	3	Ben Lomond Creek
	4	Hogarth Creek
S. secretus	5	Hop Pole Creek
	6	Trib. of Little Donaldson River
	7	Valley Creek
	8	Township Creek
	9	Bird River
	10	Cataract Creek
	11(35)*	Sorell Creek
	12(36)	Dip River
S. aquaticus	13(37)	Emu River
	14(38)	West Swan River
	15(39)	Horseshoe Bend River

* Numbers given in brackets indicate the numbers assigned to the same groups in the final analyses.

Pedder, no longer exists. The larvae had been collected in 1972 just prior to the flooding of that lake for hydro-electric power generation.

As larvae of the last instar only are morphologically distinguishable from other instars it was not possible to restrict the analysis to larvae of a particular earlier instar. The only solution, if the analysis was to proceed, appeared to be to restrict the data set, for each locality, to last instar larvae plus the remaining largest larvae (those with the greatest total length) needed to bring the sample up to 15. A minimum total length of 5.5 mm was arbitrarily set. As a consequence of this procedure some adjustment for size must be made for groups to be comparable.

Measurements Used to Describe Larval Shape

For the preliminary canonical variate analysis nine measurements were made on each of the 15 larvae in each of the 10 groups of *S. secretus* and five groups of *S. aquaticus* (Table 5.1) included in the analysis. The nine measurements consisted of three length and five width measurements on the dorsal shield as well as the maximum height of the larva in longitudinal cross-section. The position of each measurement on the larval shield is illustrated in Figure 5.1.

Collection and preservation procedures used for the larvae in both the pilot and final studies were as given in Chapter 3, Section 3.2. All measurements of larvae were made with an Mc6-1 microscope using an 8X eyepiece graticule. To ensure uniformity of measurement each larva was placed in a petri dish and just covered with 70% ethanol. Gentle pressure was applied to the dorsal surface with a pair of blunt forceps to ensure that the larva remained in position and was in contact with the bottom of the dish throughout the measuring period. To measure larval height the larva was placed, ventral surface down, on a glass slide and both larva and slide were viewed in longitudinal cross-section beneath the microscope.

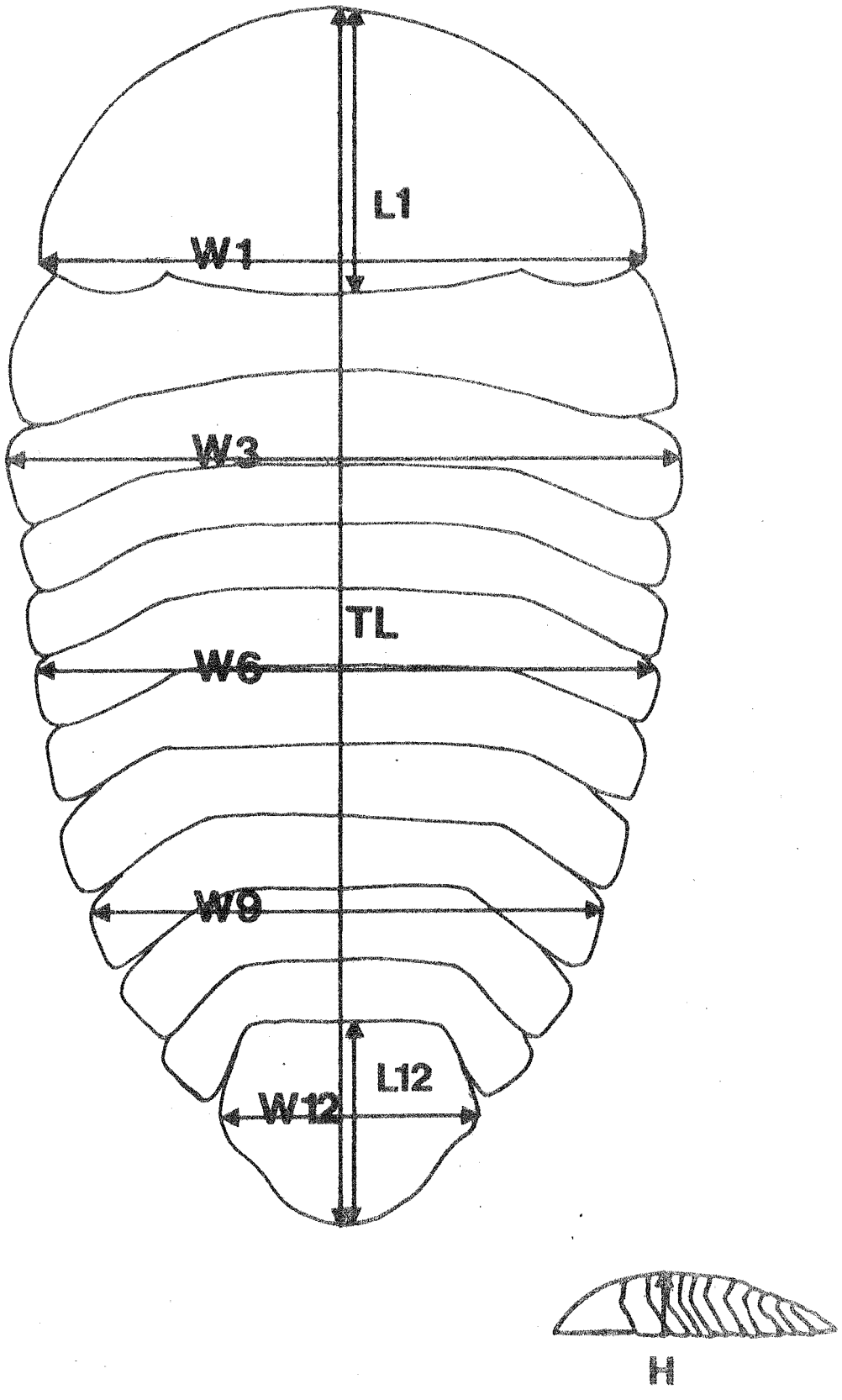


FIGURE 5.1 The nine measurements taken on each larva. TL = total length of the larval shield; L1 = length of segment 1; L12 = length of segment 12; W1, W3, W6, W9 and W12 = widths of segments 1, 3, 6, 9, and 12, respectively; H = maximum height. All measurements were in millimetres.

Testing for Measurement Error

The number of measurements made for the pilot study alone totalled 2,025. Inevitably some errors in measurement must occur where such a large number of measurements have been made. The data were checked for such errors by examining each variable separately and fitting a completely random design model using length as a covariate to adjust for size differences. The residuals from this analysis were plotted on a probability plot. Outliers in the plot were then considered to represent odd values which might have arisen through incorrect measurement. Because larvae had been retained and were available for re-measurement it was possible to compare repeat measurements made on animals with doubtful recordings, to the original measurements. The repeat measurements approximated the estimated values, in all cases, and so were substituted for the original values.

Testing for Constant Relationships Between Variables

A meaningful application of canonical variate analysis is only possible if there is a consistent pattern of interrelationships between variables over the groups being compared. Constancy of relationship between variables can be ascertained by examining the correlation matrices obtained in the canonical variate analysis. The patterns of correlations between variables must be the same for all groups. The correlation matrices obtained for the 15 groups of the pilot study were examined with this in mind.

Adjustment of Data for Size

As noted above it was not possible, in this study, to consider larvae of only one age class. Consequently there was some unavoidable variation between larvae on the basis of size and it was necessary to make an adjustment for size before groups could be compared for differences

in shape. The way in which measurements were adjusted for size, however, may considerably influence the final result of the canonical variate analysis and, therefore, the comparison of groups. For this reason, two separate canonical variate analyses were performed on the pilot data, each using a different method of adjustment for size, and the results were compared.

The methods employed were:

1. covariance analysis of width measurements using total length as the covariate. The adjusted width measurements were regarded as shape variables;

2. adjustment of width measurements by dividing each width measurement by total length.

The first method was chosen because it assumes a linear relationship; that is, an additive relationship between length and size. The second method assumes a multiplicative relationship in which size is assumed to grow proportionately with length.

5.4 Results

The correlation matrices obtained from the canonical variate analysis performed on the pilot data are given in Table 5.2. The eigen values, percentage variance explained, eigen vectors and canonical variate means for the canonical variate analysis performed on the covariance-adjusted pilot data and the total length-adjusted pilot data, using six variables (see explanation below) are given in Tables 5.3 and 5.4 respectively.

Summaries of the important features of the tables of Mahalanobis distances obtained for these two analyses are given in Tables 5.5 and 5.6 respectively. The tables of Mahalanobis distances are given in Appendix B (Tables B-1 and B-2 respectively). Graphs showing the first

TABLE 5.2 Correlation matrices for each of the ten groups of *S. secretus* and five groups of *S. aquaticus* in the pilot study.

1. *S. secretus*, Lambert Creek

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.84	1.00							
V_3	0.94	0.74	1.00						
V_4	0.95	0.82	0.90	1.00					
V_5	0.92	0.80	0.87	0.99	1.00				
V_6	0.94	0.81	0.89	0.99	0.99	1.00			
V_7	0.90	0.73	0.89	0.93	0.94	0.95	1.00		
V_8	0.75	0.77	0.72	0.80	0.83	0.81	0.77	1.00	
V_9	-0.36	-0.34	-0.29	-0.35	-0.35	-0.39	-0.43	-0.36	1.00

2. *S. secretus*, Waterworks Creek

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.75	1.00							
V_3	0.82	0.53	1.00						
V_4	0.86	0.58	0.92	1.00					
V_5	0.86	0.49	0.85	0.94	1.00				
V_6	0.88	0.61	0.87	0.97	0.95	1.00			
V_7	0.90	0.55	0.92	0.96	0.94	0.97	1.00		
V_8	0.85	0.52	0.90	0.85	0.84	0.82	0.90	1.00	
V_9	0.86	0.42	0.75	0.86	0.87	0.88	0.88	0.80	1.00

3. *S. secretus*, Ben Lomond Creek

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.75	1.00							
V_3	0.83	0.60	1.00						
V_4	0.91	0.87	0.79	1.00					
V_5	0.84	0.75	0.85	0.93	1.00				
V_6	0.65	0.52	0.54	0.70	0.69	1.00			
V_7	0.89	0.74	0.89	0.93	0.93	0.70	1.00		
V_8	0.82	0.66	0.71	0.81	0.74	0.71	0.78	1.00	
V_9	0.48	0.13	0.53	0.44	0.49	0.07	0.50	0.57	1.00

4. *S. secretus*, Hogarth Creek

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.78	1.00							
V_3	0.55	0.42	1.00						
V_4	0.94	0.83	0.61	1.00					
V_5	0.92	0.78	0.57	0.98	1.00				
V_6	0.92	0.77	0.57	0.98	0.99	1.00			
V_7	0.95	0.75	0.62	0.97	0.98	0.98	1.00		
V_8	0.83	0.74	0.32	0.84	0.84	0.82	0.80	1.00	
V_9	0.77	0.37	0.54	0.58	0.57	0.57	0.65	0.51	1.00

TABLE 5.2 (continued)

5. *S. secretus*, Hop Pole Creek

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.81	1.00							
V_3	0.84	0.78	1.00						
V_4	0.95	0.81	0.88	1.00					
V_5	0.94	0.76	0.89	0.98	1.00				
V_6	0.95	0.76	0.86	0.98	0.98	1.00			
V_7	0.96	0.83	0.86	0.98	0.97	0.98	1.00		
V_8	0.93	0.80	0.83	0.97	0.95	0.95	0.97	1.00	
V_9	0.94	0.74	0.83	0.93	0.91	0.93	0.93	0.92	1.00

6. *S. secretus*, Tributary of Little Donaldson River

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.91	1.00							
V_3	0.95	0.88	1.00						
V_4	0.89	0.95	0.90	1.00					
V_5	0.89	0.93	0.91	0.98	1.00				
V_6	0.92	0.93	0.93	0.98	0.98	1.00			
V_7	0.95	0.95	0.94	0.98	0.97	0.99	1.00		
V_8	0.95	0.90	0.90	0.92	0.92	0.96	0.96	1.00	
V_9	0.86	0.88	0.81	0.85	0.84	0.85	0.86	0.85	1.00

7. *S. secretus*, Valley Creek

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.81	1.00							
V_3	0.91	0.72	1.00						
V_4	0.87	0.81	0.89	1.00					
V_5	0.88	0.82	0.87	0.98	1.00				
V_6	0.90	0.82	0.89	0.97	0.99	1.00			
V_7	0.94	0.87	0.93	0.96	0.95	0.96	1.00		
V_8	0.93	0.86	0.92	0.92	0.91	0.93	0.96	1.00	
V_9	0.92	0.73	0.84	0.81	0.79	0.85	0.87	0.84	1.00

8. *S. secretus*, Township Creek

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.81	1.00							
V_3	0.86	0.79	1.00						
V_4	0.74	0.78	0.79	1.00					
V_5	0.81	0.88	0.85	0.88	1.00				
V_6	0.76	0.84	0.82	0.87	0.98	1.00			
V_7	0.78	0.83	0.79	0.87	0.96	0.96	1.00		
V_8	0.28	0.21	0.43	0.53	0.47	0.48	0.50	1.00	
V_9	0.69	0.57	0.57	0.57	0.58	0.53	0.55	0.19	1.00

TABLE 5.2 (continued)

9. *S. secretus*, Bird River

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.81	1.00							
V_3	0.87	0.88	1.00						
V_4	0.90	0.80	0.86	1.00					
V_5	0.91	0.72	0.81	0.95	1.00				
V_6	0.96	0.83	0.89	0.97	0.96	1.00			
V_7	0.96	0.81	0.89	0.96	0.95	0.99	1.00		
V_8	0.84	0.66	0.80	0.89	0.88	0.91	0.91	1.00	
V_9	0.72	0.45	0.58	0.67	0.66	0.74	0.78	0.80	1.00

10. *S. secretus*, Cataract Creek

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.84	1.00							
V_3	0.94	0.74	1.00						
V_4	0.95	0.82	0.90	1.00					
V_5	0.92	0.80	0.87	0.99	1.00				
V_6	0.94	0.81	0.89	0.99	0.99	1.00			
V_7	0.90	0.73	0.89	0.93	0.94	0.95	1.00		
V_8	0.75	0.77	0.72	0.80	0.83	0.81	0.77	1.00	
V_9	0.85	0.58	0.79	0.81	0.78	0.83	0.85	0.58	1.00

11. *S. aquaticus*, Sorell Creek

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.96	1.00							
V_3	0.94	0.90	1.00						
V_4	0.95	0.95	0.90	1.00					
V_5	0.95	0.96	0.90	0.99	1.00				
V_6	0.95	0.95	0.90	0.99	0.99	1.00			
V_7	0.96	0.96	0.92	0.99	0.99	0.99	1.00		
V_8	0.96	0.92	0.95	0.93	0.93	0.93	0.94	1.00	
V_9	0.91	0.85	0.92	0.85	0.85	0.86	0.88	0.91	1.00

12. *S. aquaticus*, Dip River

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.95	1.00							
V_3	0.38	0.43	1.00						
V_4	0.96	0.96	0.41	1.00					
V_5	0.97	0.96	0.39	0.99	1.00				
V_6	0.98	0.96	0.37	0.99	0.99	1.00			
V_7	0.98	0.96	0.36	0.98	0.99	0.99	1.00		
V_8	0.98	0.95	0.38	0.96	0.97	0.98	0.97	1.00	
V_9	0.94	0.91	0.42	0.90	0.91	0.93	0.92	0.93	1.00

TABLE 5.2 (continued)

13. *S. aquaticus*, Emu River

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.88	1.00							
V_3	0.55	0.68	1.00						
V_4	0.92	0.88	0.46	1.00					
V_5	0.91	0.88	0.51	0.99	1.00				
V_6	0.85	0.84	0.42	0.96	0.94	1.00			
V_7	0.93	0.91	0.52	0.96	0.95	0.95	1.00		
V_8	0.89	0.87	0.56	0.95	0.95	0.91	0.96	1.00	
V_9	0.78	0.72	0.35	0.87	0.87	0.80	0.85	0.90	1.00

14. *S. aquaticus*, West Swan River

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.83	1.00							
V_3	0.85	0.65	1.00						
V_4	0.86	0.75	0.86	1.00					
V_5	0.88	0.76	0.90	0.97	1.00				
V_6	0.93	0.78	0.90	0.96	0.97	1.00			
V_7	0.90	0.78	0.85	0.97	0.95	0.97	1.00		
V_8	0.90	0.79	0.92	0.96	0.98	0.98	0.97	1.00	
V_9	0.94	0.76	0.80	0.83	0.82	0.90	0.89	0.86	1.00

15. *S. aquaticus*, Horseshoe Bend Creek

	V_1	V_2	V_3	V_4	V_5	V_6	V_7	V_8	V_9
V_1	1.00								
V_2	0.95	1.00							
V_3	0.97	0.92	1.00						
V_4	0.99	0.96	0.96	1.00					
V_5	0.98	0.96	0.96	0.99	1.00				
V_6	0.99	0.96	0.96	0.99	0.99	1.00			
V_7	0.99	0.96	0.97	0.99	0.99	0.99	1.00		
V_8	0.98	0.94	0.97	0.97	0.97	0.97	0.98	1.00	
V_9	0.95	0.87	0.92	0.93	0.93	0.93	0.94	0.95	1.00

TABLE 5.3 Results of canonical variates analysis performed on the covariance-adjusted data of the pilot study.

Canonical Variables		1	2	3
Eigen Values		2.72	2.42	0.53
Percentage Variance Explained		43.57	38.72	8.58
Eigen Vectors				
	V_1	-7.99	25.19	98.55
	V_2	-10.28	26.30	100.02
	V_3	-10.86	22.32	99.22
	V_4	-11.73	25.76	98.06
	V_5	-8.13	13.36	97.82
	V_6	0.49	17.64	103.40
Canonical Variate Means	*1	2.43	-1.15	-1.38
	2	1.43	0.30	0.14
	3	2.91	1.34	1.16
	4	-0.21	0.26	-0.26
	5	1.97	-1.77	1.15
	6	1.09	2.79	-0.23
	7	-1.27	2.72	-0.37
	8	-0.29	0.14	-0.59
	9	0.11	0.21	-0.38
	10	-2.54	1.48	0.11
	11	-1.50	-1.13	0.36
	12	-0.89	-0.44	0.15
	13	-1.91	-0.79	1.10
	14	-1.26	-1.95	-0.11
	15	-0.04	-2.02	-0.84

* locality groups: 1-10, *S. secretus;* 11-15, *S. aquaticus.*

TABLE 5.4 Results of canonical variates analysis performed on the total length-adjusted data of the pilot study.

Canonical Variables		1	2	3
Eigen Values		2.59	2.46	0.31
Percentage Variance Explained		45.39	43.22	5.53
Eigen Vectors				
	V_1	-27.32	236.04	-289.10
	V_2	-76.65	258.93	-39.57
	V_3	-82.57	157.13	-322.09
	V_4	-141.51	214.56	-414.02
	V_5	52.90	-60.97	-301.35
	V_6	176.74	-37.58	34.73
Canonical Variate Means	*1	3.94	-0.71	0.84
	2	0.93	0.81	-0.57
	3	1.64	1.96	-0.04
	4	-0.13	0.22	-0.42
	5	1.46	-0.87	-0.05
	6	0.36	2.98	-0.56
	7	-1.64	2.21	-0.01
	8	-0.16	0.09	-0.29
	9	0.09	0.27	0.94
	10	-2.49	0.74	1.01
	11	-1.17	-1.42	0.45
	12	-0.86	-0.69	-0.23
	13	-1.58	-0.98	0.02
	14	-0.95	-2.20	-0.58
	15	0.57	-2.42	-0.48

* locality groups: 1-10, *S. secretus*; 11-15, *S. aquaticus*.

TABLE 5.5 Summary of the important features of the table of Mahalanobis distances (Table B-1) obtained for the canonical variate analysis on the covariance-adjuste data set of the pilot study.

Groups which are not significantly different in larval shape (Pairs of groups with M-distance <1.5)

4, 8;	4, 12;
8, 9;	8, 12;
11, 12	

Groups which differ, significantly, from all others on the basis of larval shape

1, 2, 3, 5, 6, 7, 10, 13, 14, 15

TABLE 5.6 Summary of the important features of the table of Mahalanobis distances (Table B-2) obtained for the canonical variate analysis on the total-length-adjusted data of the pilot study.

Groups which are not significantly different in larval shape (Pairs of groups with M-distance <1.4)

2, 8	
4, 8	
8, 9;	8, 12
11, 12	
12, 13	

Groups which differ significantly from all others on the basis of larval shape

1, 3, 5, 6, 7, 10, 14, 15

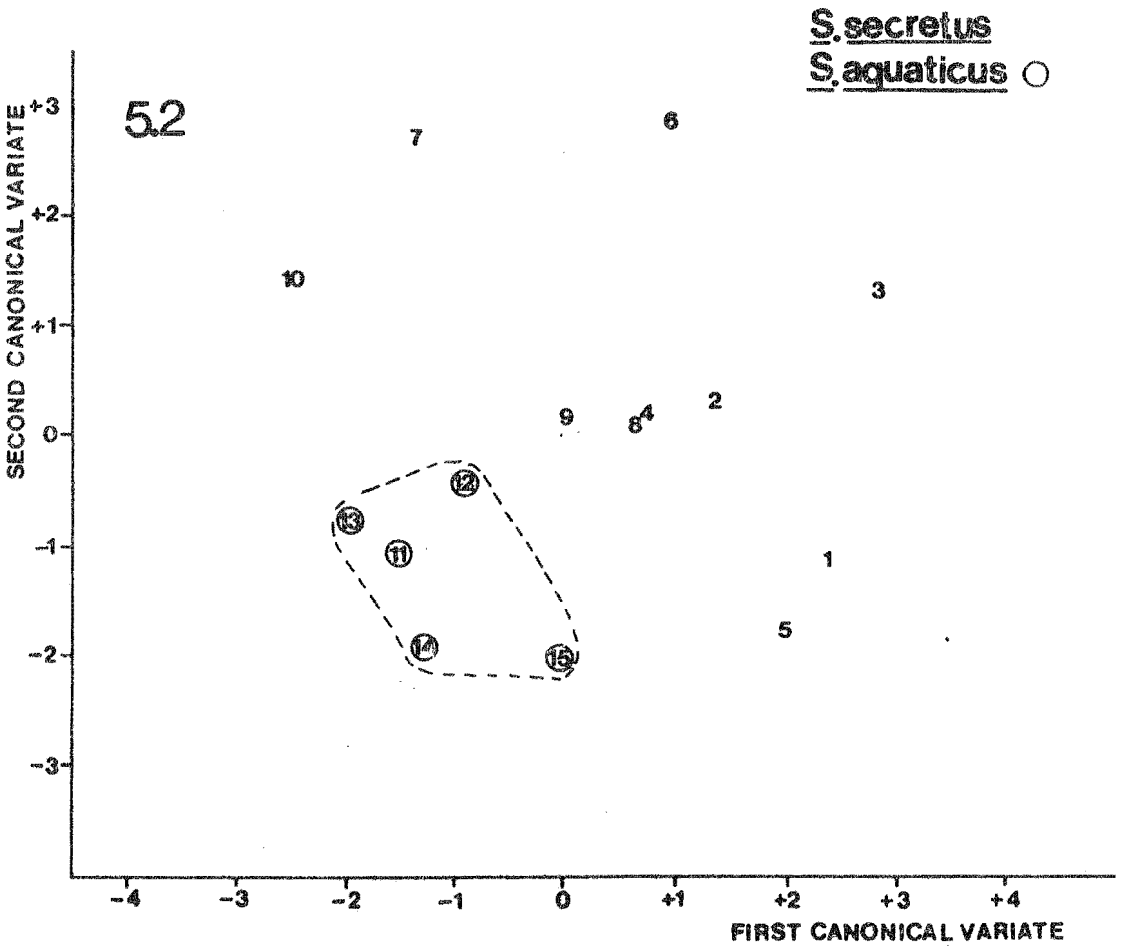
canonical variate plotted against the second, for both analyses, are given in Figures 5.2 and 5.3 respectively.

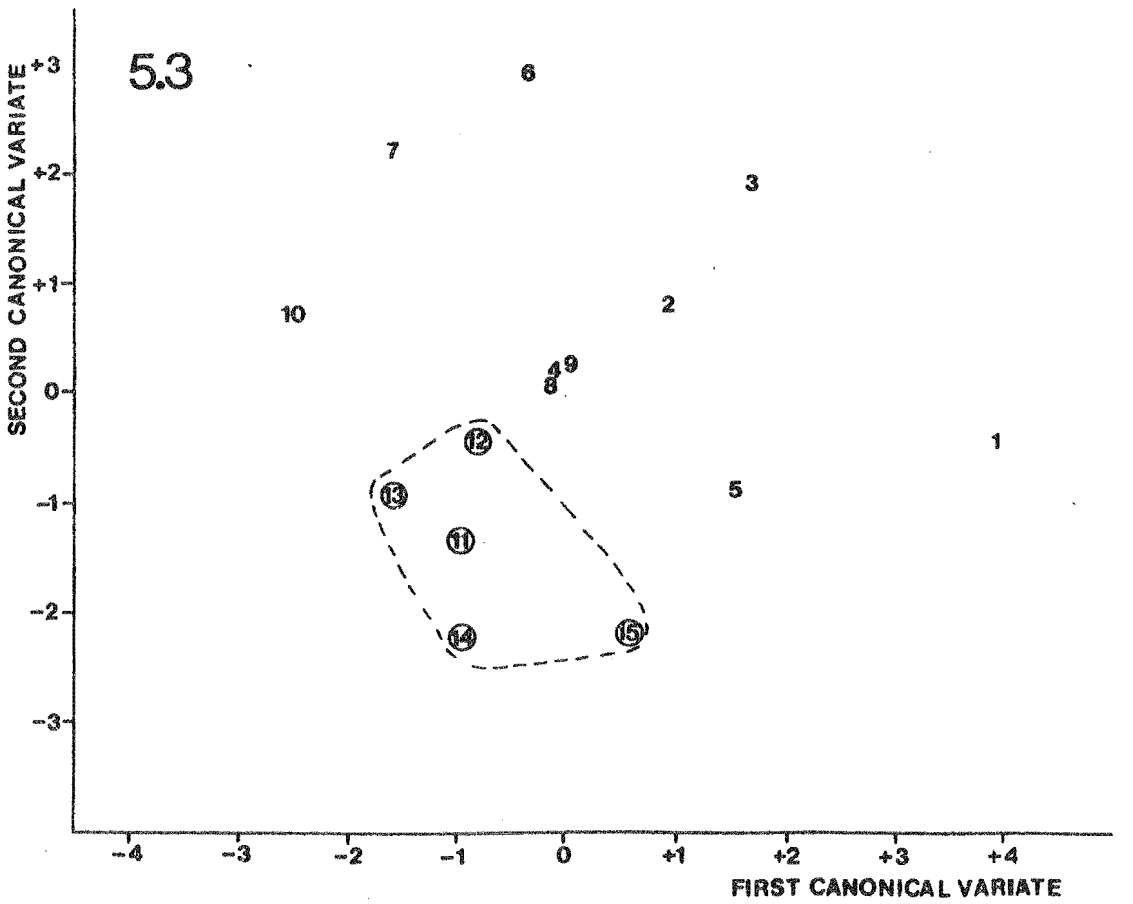
5.5 Discussion

Examination of the correlation matrices obtained for the canonical variate analysis performed on the pilot data using nine variables (Table 5.2) revealed that three of the variables did not display a consistent pattern of relationships over groups being compared. These were; variable 2, the length of the first segment (L_1), variable 3, the length of segment 12 (L_{12}), and variable 9, height (H). Inconsistent correlations are underlined in Table 5.2. These three variables were discarded from subsequent analyses leaving only the following six; total length (TL), width of segment I (WI), width of segment 3 (W3), width of segment 6 (W6), width of segment 9 (W9) and width of segment 12 (W12). The high correlations in each of these latter six variables, over all groups, revealed that the interrelationships between shapes in each group, as determined by the measured variables, were extremely uniform. Such uniformity indicated that 15 larvae per group was a reasonable number of larvae to work with given the difficulties involved in using larger groups (Section 5.3).

Examination of Tables 5.3-5.6 and Figures 5.2 and 5.3 reveals only small differences in the distances between pairs of groups in the canonical variate analysis performed on the covariance adjusted data and that performed on the total length adjusted data. This suggests that the results of the study were not likely to be dependent on the method of adjustment for size.

The subsequent final canonical variate analyses were based on a refinement of the second multiplicative method since this was computationally simpler. Size was related to area and defined according to the formula,





FIGURES 5.2-5.3 Canonical variate analysis on the pilot study data comprising ten groups of *S. secretus* (1-10) and five groups of *S. aquaticus* (11-15) using: (5.2) covariance-adjusted data; (5.3) total length-adjusted data. The five groups of *S. aquaticus* are enclosed within the dotted line.

$$\text{Size} = \log[TL \times \frac{1}{5}(W_1 + W_3 + W_6 + W_9 + W_{12})]$$

Shape was then defined as the set of five variables formed by transforming each width measurement according to the formula,

$$\text{shape} = \log\ (\frac{W}{\text{size}})$$

Comparison of Figures 5.2 and 5.3 with the graphs obtained for the final canonical variate analyses (Section 5.7, Figures 5.8 and 5.10) revealed few differences in the distances between groups under all three methods of size adjustment. The analyses were, in fact, extremely robust under all three transformations for size. The formula relating size to area was used in the final study as it did not associate size with only one dimension (total length) but rather with area and therefore probably represented the most valid means of adjusting for size.

Final Study

5.6 Materials and Methods

Canonical Variate Analysis on Total Data Set (41 groups)

Two canonical variate analyses were performed on a total data set comprising six measurements per larvae for 15 larvae in each of 41 locality groups. These groups consisted of 34 groups of *S. secretus*, six groups of *S. aquaticus* and one of *S. lacustris*. The localities are listed in Table 5.7 and marked on the map of Tasmania in Figure 5.4. The ten groups of *S. secretus* and five groups of *S. aquaticus* in the pilot study were included within the 41 groups of the final study.

The choice of groups, the size of larvae within each group, the method of measurement and the method of adjustment for size in this final study were all as described and discussed in the pilot study.

The two analyses were based on a set of six variables and five variables respectively. The set of six variables comprised one size

TABLE 5.7 The number, name and map reference of locality-groups of *S. secretus* (34), *S. aquaticus* (6) and *S. lacustris* (1) included in the final analysis. Map references are for the Tasmaps 1:100 000 series, Lands Department, Hobart, and comprise the four figure sheet number plus a six figure grid reference.

Species	Number	Locality	Map Reference	
	1	Lambert Creek	8312	269490
	2	Waterworks Creek	8312	230490
	3	Ben Lomond Creek	8414	539045
	4	Hogarth Creek	7916	716634
	5	Hop Pole Creek	8514	838661
	6	Trib. of the Little Donaldson River	7915	546217
	7	Valley Creek	8013	932385
	8	Township Creek	8013	859231
	9	Bird River	8012	838111
	10	Cataract Creek	8012	926859
S. secretus	11	Parsons Bay Creek	8411	609271
	12	Pawleena Creek	8412	484699
	13	Browns River	8312	207475
	14	Browns River	8312	207475
	15	Baxter River	8013	874281
	16	Baxter River	8013	874281
	17	Pearl Creek	8013	782444
	18	Pearl Creek	8013	782444
	19	Parsons Bay Creek	8411	609271
	20	Runnel in the Olga R. catchment	8012	989692
	21	Myrtle Forest Creek	8312	128545
	22	Newtown Rivulet	8312	189519
	23	Creek in gully west of Cox's Ridge	8012	022698
	24	Creek near Gordon Dam	8112	186643
	25	Tyndall Ranges Creek	8014	815578
	26	Hannant Inlet Creek	8011	187997
	27	Mt. Barrow Creek	8315	361211
	28	Dee River	8213	681180
	29	Meredith River	8513	869362
	30	Lake Pedder	8112	338435

TABLE 5.7 (continued)

Species	Number	Locality	Map Reference	
S. secretus	31	Un-named creek on right bank of Gordon River	8012	998734
	32	Un-named creek on right bank of Gordon River	8012	998734
	33	Hytten Hall Creek	8312	265491
	34	Myrtle Forest Creek	8312	128545
	35	Sorell Creek	8312	129609
	36	Black River	7916	592666
	37	Emu River	8015	989304
S. aquaticus	38	West Swan River	8414	791605
	39	Horseshoe Bend Creek	8513	850261
	40	Liffey River	8214	842854
S. lacustris	41	Lake Sorell	8313	148338

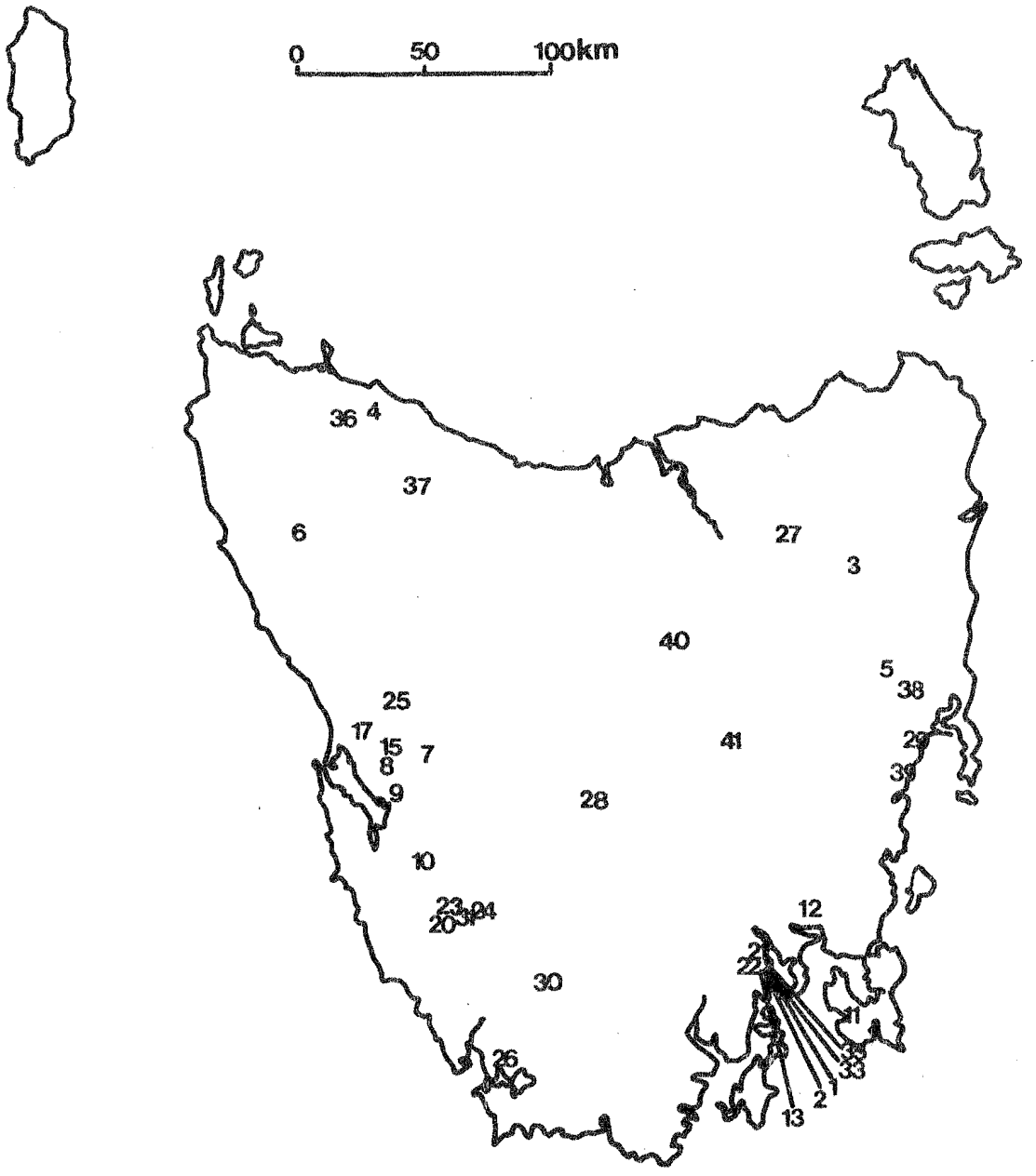


FIGURE 5.4 Map of Tasmania showing the locations of the 41 groups of the total data set comprising 34 groups of *S. secretus* (1-34), six groups of *S. aquaticus* (35-40) and one group of *S. lacustris* (41). The name and map reference of each group is given in Table 5.7. Where two groups were collected from the same locality (five instances) only the lower number of the two is marked on the map.

variable, V_1, where;

$$V_1 = \log[TL \times \frac{1}{5}(W_1 + W_3 + W_6 + W_9 + W_{12})]$$

and five shape variables $V_2 - V_6$ where;

$$V_2 = \log \frac{W_1}{V_1}, \quad V_3 = \log \frac{W_3}{V_1}, \quad V_4 = \log \frac{W_6}{V_1}, \quad V_5 = \log \frac{W_9}{V_1},$$

$$V_6 = \log \frac{W_{12}}{V_1}$$

The reasons for choosing these transformations are given in Section 5.5. The set of five variables comprised the five shape variables $V_2 - V_6$ as defined above.

The two analyses were performed to allow comparative studies of distances between groups based on the use of different data sets. By comparing the results obtained using six variables with those obtained using five it was possible to assess whether size differences between different localities were significant in distinguishing any groups.

Canonical Variate Analysis on the Single Species, *S. secretus* (34 groups)

Two canonical variate analyses based on the sets of six variables and five variables respectively (described above) were also performed on a data set comprising the set of 34 groups of *S. secretus* only. This was done to determine whether the same pattern of differences between localities was maintained for the single species, *S. secretus* , (which comprised the largest number of groups in the analyses) when the groups for the other two species, *S. aquaticus* and *S. lacustris*, were removed.

Testing for Sampling Error Using Two Groups from the Same Locality

The procedures of statistical inference employed in analysis of the data assumed that the larvae within each group were randomly selected. In this study, however, it was often neither possible nor practical to attempt to define a random sampling procedure. Hence there

was sone concern that differences between groups might in fact be attributable sampling procedures rather than population differences. For this reason two groups of 15 animals were taken from each of five different localities and included in the analysis. An examination of M-distances between each pair of groups would then provide an indication of whether groups within the same locality were distinguishable with regard to shape.

The five localities from which duplicate groups were taken were; Parson's Bay Creek (11,19), Browns River (13,14), Baxter Rivulet (15,16), Pearl Creek (17,18) and an un-named creek on the right bank of the Gordon River, above the Olga River junction (31,32). The numbers of the groups are given in brackets. All groups contained *S. secretus* larvae.

Testing for Measurement Error Using the Same Group of Larvae Measured Twice

Because larvae were labelled and stored after measurement it was possible to remeasure animals at a later date. This offered a means of assessing the extent of measurement error. The same set of larvae of *S. secretus* from one locality, Myrtle Forest Creek, were measured on two different occasions and included within the canonical variate analyses as distinct groups, 21 and 34. By the use of the test based on M-distances it was possible to determine whether the groups were sufficiently close to be regarded as coming from the same population.

Testing for Distinct Subgroups Within Each Group

From the results of the pilot study (examination of the correlation matrices) it was assumed that the variability within each group was fairly uniform over all groups included in the analysis. An attempt was made to further test the validity of this assumption by the use of two statistical procedures.

Firstly, a cluster analysis was performed on the set of larval

measurements within each group. Cluster analysis is a technique by which individuals or groups are brought together, by virtue of common properties, into a cluster which is then considered to differ from all other similarly developed clusters. However, such clusters can be further grouped, on the basis of common properties, until finally a single, ultimate group is formed.

Rao (1952) noted that there is no clear definition of a cluster. A large number of clustering methods are now available but, as noted by Blackith and Reyment (1971), different clustering methods may well result in different geometrical distributions of the same original data set.

The clustering method used here was Ward's method which is a useful intermediate method between furthest neighbour and nearest neighbour methods. While the analysis of each locality is of little value in isolation by comparing the levels at which clusters form in different localities it is possible to detect a locality in which the final grouping forms at a substantially different level from the norm.

The second process involved the use of univariate analysis of variance to obtain the variance for each variable from the set of 15 measurements within each group. The function of variance calculations is to detect distinct groupings within a locality by an inflated variance which is likely to have resulted from the existence of distinct and well-separated groups.

Correlations Between Canonical Variables and Environmental Variables

Having determined the relative position of groups with respect to shape, using canonical variate analysis, an attempt was made to explain the pattern by reference to environmental factors. Eleven environmental factors were chosen for study primarily on the basis of whether data for each factor was available for each of the 41 groups included in the canonical variate analysis. As ten of these factors were represented by

continuous variables it was possible to calculate correlation coefficients (r) for these variables and the set of means on each canonical variate axis for the total data set of 41 localities. For the discontinuous variable, substrate, two way contingency tests were carried out to determine whether a significant relationship existed between the variable and the three canonical variates.

The canonical variate means used were those listed in Table 5.11. The eleven environmental variables are described below and the value of each variable, in each locality, is listed in Table 5.8.

Stream Order, Number of Tributaries and Stream Length

Stream order was calculated using Strahler's (1957) modification of Horton's (1945) system of drainage analysis. Stream order may be defined as a measure of the position of a stream in a hierarchy of tributaries (Leopold *et al.*, 1964). First order streams are those which have no tributaries, second order streams are those which have only first order streams as tributaries and third order streams receive both first and second order streams as tributaries (Leopold *et al.*, 1964). Streams of higher orders are similarly defined. Horton (1945) considered that each higher order stream extended to the tip of the longest tributary it drained. Strahler (1957) simplified Horton's approach to stream order by restricting the designation of order to stream segments. This overcame the difficulty of renumbering a tributary when high order streams were recognised. Although the number of tributaries of a stream and its length are related to stream order by simple geometric relationships (Horton, 1945) they were included within the analysis as they may contribute extra information to that provided by stream order alone.

Values for the three variables were calculated using the exact position of each locality on maps of the 1:100 000 Tas maps series, published by the Lands Department, Hobart.

TABLE 5.8 Values of selected environmental variables for each group in the total data set (41 groups).

Groups		Environmental Variables										
Locality Number and Name		Stream Order	Number of Tributaries	Stream Length (km)	Altitude (m)	Rainfall Mean per Annum (mm)	Rainfall Variability	Air Temperature (°C)				Substrate*
								January		July		
								Mean Max.	Mean Min.	Mean Max.	Mean Min.	
		E_1	E_2	E_3	E_4	E_5	E_6	E_7	E_8	E_9	E_{10}	E_{11}
1	Lambert Creek	1	0	2.0	40	626	0.23	22	16.4	8.1	4	D
2	Waterworks Creek	1	0	0.4	380	1,235	0.20	22	15	6.4	4	D
3	Ben Lomond Creek	1	0	0.2	1,180	1,344	0.25	21	9.7	3	0	D
4	Hogarth Creek	1	0	2.2	80	1,164	0.18	21	16.4	6.4	3	Q
5	Hop Pole Creek	2	2	1.8	290	565	0.25	19	13	6.4	3	D
6	Trib. of Little Donaldson River	1	0	1.6	480	2,011	0.16	22	13	4.7	3	Q
7	Valley Creek	1	0	1.4	360	2,443	0.13	19	15	6.4	4	A
8	Township Creek	2	6	2.2	190	2,443	0.13	19	15	6.4	4	A
9	Bird River	3	11	9.6	140	1,973	0.13	19	15	6.4	4	A
10	Cataract Creek	3	10	7.6	100	2,600	0.13	19	15	6.4	4	Q
11	Parsons Bay Creek	3	15	10.2	2	811	0.23	19	15	8.1	4	D
12	Pawleena Creek	1	5	3.9	90	599	0.23	20	16.4	6.4	4	D
13	Browns River	1	0	0.8	400	1,235	0.2	23	15	6.4	3	D
14	Browns River	1	0	0.8	400	1,235	0.2	23	15	6.4	3	D
15	Baxter Rivulet	1	0	1.4	190	2,443	0.13	19	15	6.4	4	A
16	Baxter Rivulet	1	0	1.4	190	2,443	0.13	19	15	6.4	4	A
17	Pearl Creek	1	0	2.2	120	2,416	0.13	19	15	6.4	4	A
18	Pearl Creek	1	0	2.2	120	2,416	0.13	19	15	6.4	4	A
19	Parsons Bay Creek	3	15	10.2	2	811	0.23	19	15	8.1	4	D
20	Runnel in the Olga Catchment	1	0	0.4	140	3,400	0.13	19	15	6.4	4	Q
21	Myrtle Forest Creek	1	0	1.4	620	1,200	0.20	22	15	6.4	2	D
22	Newtown Rivulet	1	0	0.4	800	1,200	0.20	21	13	4.7	3	D
23	Un-named creek in gully west of Cox's Ridge	1	0	0.4	180	2,600	0.13	19	15	6.4	4	Q
24	Creek near Gordon Dam	1	0	0.4	340	2,570	0.13	19	13	4.7	4	Q

TABLE 5.8 (continued)

		E_1	E_2	E_3	E_4	E_5	E_6	E_7	E_8	E_9	E_{10}	E_{11}
25	Tyndall Ranges Creek	1	0	3.0	520	2,600	0.13	19	15	4.7	3	Q
26	Hannant Inlet Creek	1	0	0.8	40	2,200	0.13	19	15	8.1	3	Q
27	Mt. Barrow Creek	1	0	0.2	900	1,445	0.25	22	9.7	4.7	0	D
28	Dee River	1	0	0.5	660	911	0.21	18	13	3	0	D
29	Meredith River	4	35	200	2	618	0.28	22	16.4	8.1	4	D
30	Lake Pedder	-	-	-	330	2,570	0.13	19	13	4.7	3	Q
31	Un-named creek on right bank of Gordon River, above the Olga River jn.	1	0	0.4	40	2,600	0.13	19	15	6.4	5	Q
32	Un-named creek on right bank of Gordon River, above the Olga River jn.	1	0	0.4	40	2,600	0.13	19	15	6.4	5	Q
33	Hytten Hall Creek	1	0	1.2	40	626	0.23	22	16.4	8.1	4	D
34	Myrtle Forest Creek	1	0	1.4	620	1,200	0.20	22	15	6.4	2	D
35	Sorell Creek	3	19	11.5	90	1,200	0.20	22	15	6.4	2	D
36	Black River	4	35	24.2	80	1,429	0.20	19	15	6.4	3	D
37	Emu River	4	38	24.8	380	1,598	0.20	19	15	6.4	3	D
38	West Swan River	4	25	20.8	100	866	0.25	22	15	6.4	3	D
39	Horseshoe Bend Creek	3	7	44	20	618	0.28	22	16.4	8.1	4	D
40	Liffey River	4	24	14.2	320	1,104	0.20	19	13	3	1	D
41	Lake Sorell	-	-	-	840	702	0.23	19	11.4	3	0	D

* Key to substrates

A = Alluvials (sandstone, mudstones and shale)
D = Dolerite
Q = Quartzite

Altitude

The altitude of each locality was also determined from the maps of the 1:100 000 Tas maps series.

Rainfall

The average annual rainfall for a number of localities was obtained from records provided by the Tasmanian Bureau of Meteorology. Where localities were not represented in the records rainfall was estimated from the map of average annual rainfall distribution in Tasmania (after Bureau of Meteorology, 1979), given in Figure 5.5.

Rainfall Variability

The relative variability of rainfall at each locality was estimated from the map of relative variability of rainfall in Tasmania, as measured by the coefficient of variability, given by Watson and Wylie (1972),

Temperature

Although weekly maximum and minimum water temperatures had been recorded in two streams near Hobart, it was not possible to take similar readings of stream temperatures for all other localities included in the multivariate analysis. Consequently air, rather than water temperatures, were used and four mean air temperatures; the January and July maxima and minima, were estimated, for each locality, from the maps of isotherms given by Langford (1965). These four temperature variables however, were viewed with caution as they may well be too crude to give an accurate picture of the temperature regime experienced within each locality.

The weekly stream maxima and minima for Lambert Creek (1) and Browns River (13,14) are given in Figures 5.6 and 5.7.

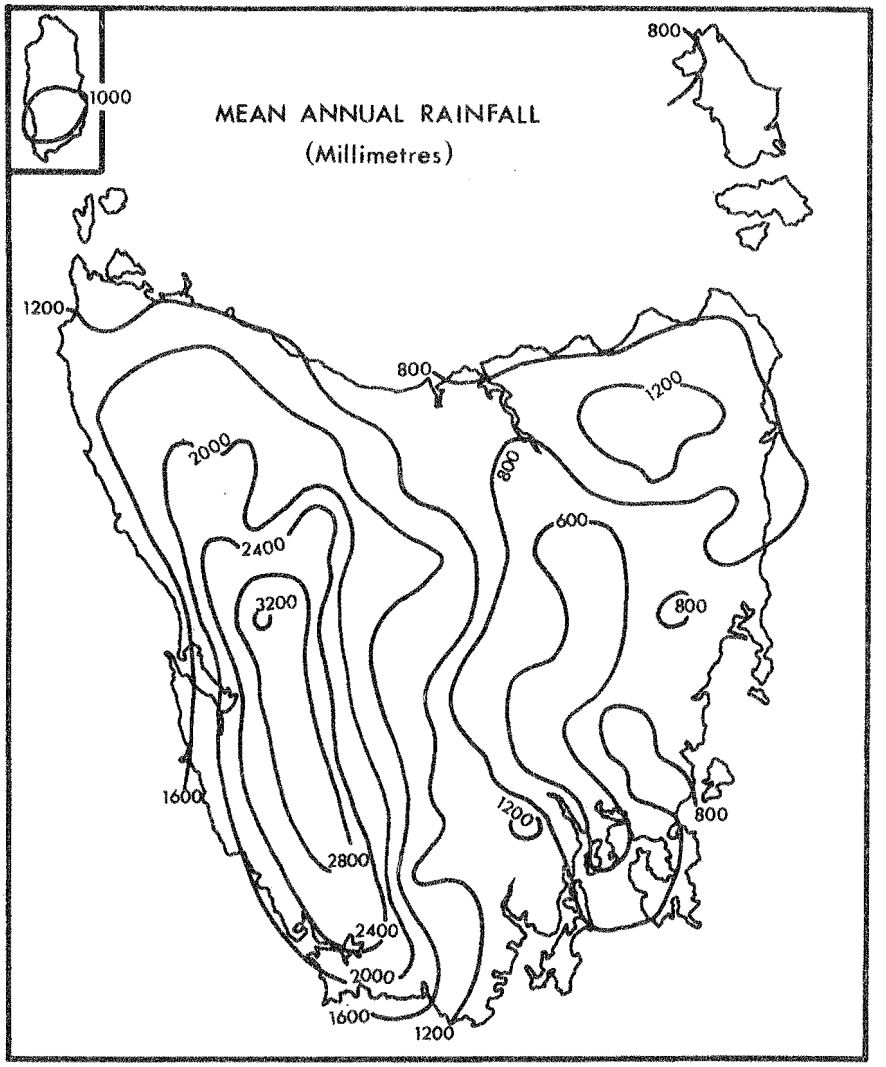
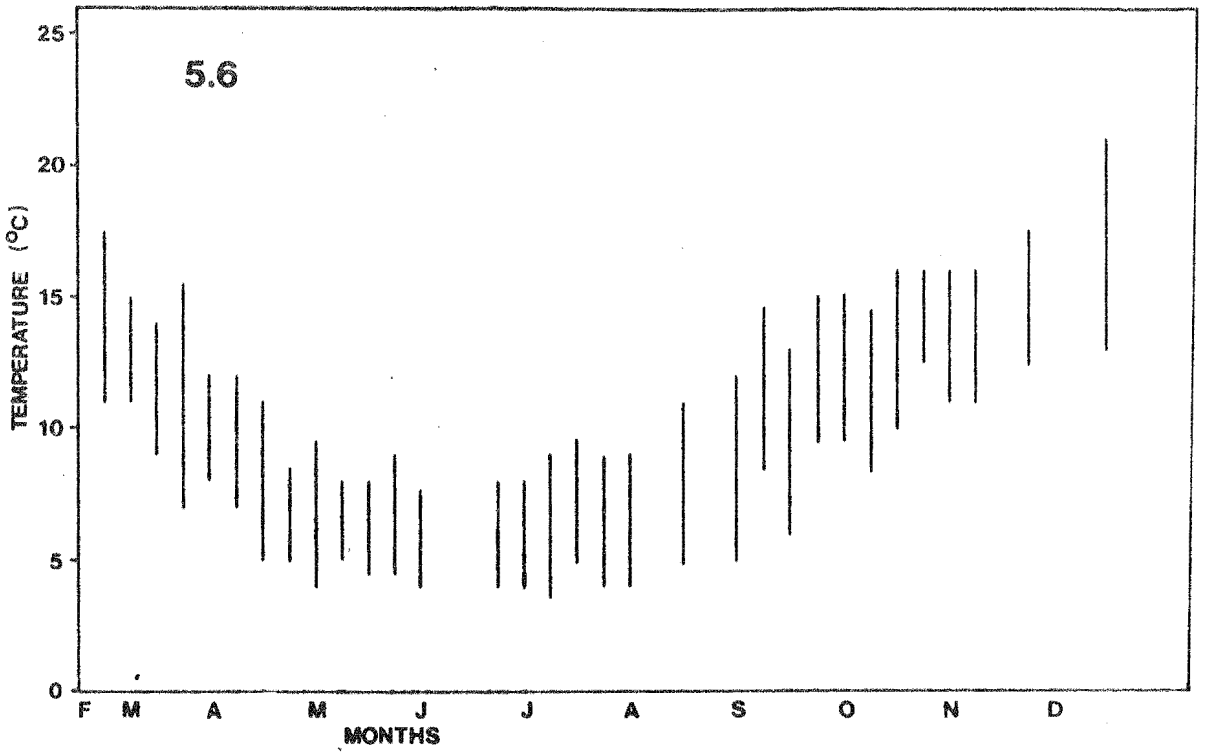
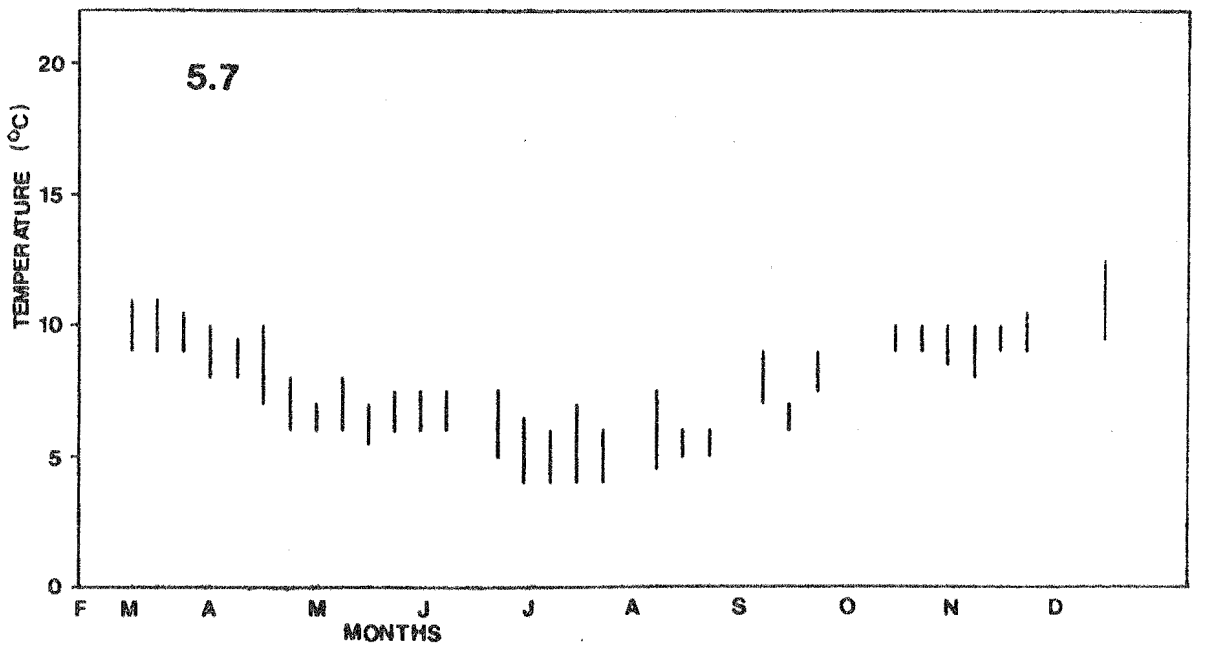


FIGURE 5.5 Rainfall map of Tasmania (from Bureau of Meteorology, 1979).





FIGURES 5.6-5.7 Weekly maximum and minimum temperatures in: (5.6) Lambert Creek; (5.7) Browns River, for the 11 month period, February to December, 1979.

Substratum

The composition of the substratum in each locality was noted at the time of sampling and three general categories are included in Table 5.8. These are; dolerite, quartzite and alluvials (sandstones, mudstones and shales). The first category included both doleritic and basaltic substrates while the last category effectively included all substrates not included in the first two.

Three Dimensional Graphs, Rainfall and Substrate

Three dimensional graphs were constructed in an attempt to further elucidate the relationship between environmental factors and the relative positions of groups, as determined by shape, in the canonical variate analysis. The graphs were constructed using perspex base plates, brass rods and coloured beads. The first and second canonical axes were represented by the x and y planes, respectively, on the base plate. The third canonical axis was represented by the z, or vertical, plane as denoted by the brass rods.

One graph was constructed for the canonical variate analysis performed on the total data set of 41 groups and one for the canonical variate analysis performed on the *S. secretus* data set of 34 groups, only. Beads were used on the end of each rod to denote the mean position of each group as determined by larval shape. Beads of different colours were used to denote both the rainfall regime and the substratum of each locality on the graph for the total data set while the rainfall regime, only, of each locality was denoted on the graph for *S. secretus* alone.

Initially beads of different colours were used to denote all environmental variables (11) considered so far, on the graphs. However only rainfall and substratum were presented in the final graphs as these gave the clearest patterns of groups in the analyses.

Mean Water Velocities

As running water is a major feature of the habitat of larval *Sclerocyphon* it was obvious that a knowledge of mean velocities occurring in each locality would be of considerable value in the interpretation of the effect of the environment on the expression of larval shape. As actual stream velocity measurements for the 41 localities included in the final study were not available mean velocities were computed using Mannings equation.

Smith (1975) notes that detailed analysis of the vast variety of flow conditions that can occur in rivers and streams is virtually impossible; however mean velocities can be computed using Manning's equation where

$$\bar{V} = \frac{1}{n} R^{\frac{2}{3}} S^{\frac{1}{2}}$$

and $\bar{V}$ = mean velocity (which occurs at approximately 0.4 depth from the bed)

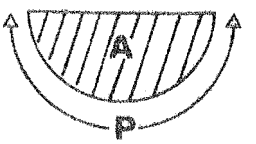
n = Manning's roughness coefficient

R = hydraulic mean radius

S = slope

The hydraulic mean radius,

$$R = \frac{P}{A}$$



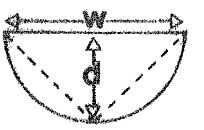
where P = wetted perimeter of stream

A = cross-sectional area of stream

In this study $P = 2\sqrt{(\frac{W}{2})^2 + d^2}$

$A = \frac{1}{2} wd$

and therefore $R = \frac{wd}{4\sqrt{(\frac{W}{2})^2 + d^2}}$



w = width of stream

d = depth of stream

Manning's equation was used to calculate mean velocities for localities where the slope,depth and width of the stream were known. As these parameters were not known for all localities (41) included in the final study calculations of correlation coefficients between mean velocities and canonical variate means, in a fashion similar to that performed on the eleven environmental variables, given above, were not attempted.

Mannings n provides an estimate of the roughness of the substratum and a value of 0.03 (after Chow, 1959) was used in all calculations of mean velocities although it is realised that bed roughness did vary between different localities.

5.7 Results

Canonical Variate Analysis on the Total Data Set (41 groups)

The results of the canonical variate analysis performed on the total data set of 41 groups using six variables are given in Table 5.9 and the results for the analysis using five variables are given in Table 5.10. The tables of Mahalanobis distances for both analyses are given in Appendix B (Tables B.3 and B.4, respectively). Using the M-distance test described in Section 5.2 the critical distances for the six variable and five variable analyses are 1.5 and 1.4 respectively. Summaries of the important features of the tables of Mahalanobis distances (Tables B.3 and B.4) are given in Tables 5.11 and 5.12 respectively.

Comparison of the results provided in Tables 5.9-5.12 suggest that size is not of any significance in distinguishing groups. The distances between groups are fairly similar under both analyses and it is apparent from a consideration of the coefficients defining the transformation of the original variables to canonical variables (the eigen vectors) that the size variable makes little contribution on any axis.

TABLE 5.9 Results of canonical variates analysis performed on total data set (41 groups), using six variables (one size and five shape variables)

Canonical Variables		1	2	3
Eigen Values		4.41	1.90	1.08
Percentage Variance Explained		52.65	22.71	12.91
Eigen Vectors	V_1	-5.49	2.78	4.02
	V_2	-16.68	45.57	36.61
	V_3	-7.25	-3.07	7.37
	V_4	-55.02	-21.80	-42.38
	V_5	38.13	-63.67	19.51
	V_6	42.81	4.36	3.93
Canonical Variate Means	*1	-2.92	-0.87	-1.07
	2	-0.58	-0.10	1.32
	3	-1.67	-1.00	2.16
	4	0.88	0.68	0.99
	5	-2.05	1.10	0.51
	6	0.73	-1.92	2.15
	7	2.96	-0.94	1.23
	8	0.99	0.44	0.39
	9	0.60	-0.13	-0.19
	10	3.30	0.31	0.03
	11	-1.32	1.03	0.72
	12	-4.25	1.20	0.44
	13	-0.14	-0.21	0.27
	14	-0.34	-0.79	0.07
	15	-0.62	-0.69	-0.67
	16	-2.00	-1.50	-0.92
	17	-0.90	-1.20	-0.91
	18	-1.49	-1.98	-1.74
	19	-1.49	1.00	0.82

TABLE 5.9 (continued)

	Canonical Variate Means		
20	3.32	-1.24	-0.42
21	-0.09	-0.60	0.87
22	0.68	-0.52	-0.07
23	2.76	-0.64	-1.08
24	2.56	0.85	-1.38
25	0.30	-0.11	-0.94
26	2.32	-0.84	-2.71
27	-0.72	-1.24	0.60
28	-2.70	0.10	-0.70
29	-3.63	1.97	-1.49
30	-2.18	-3.88	-0.11
31	3.57	-0.53	0.59
32	3.66	-0.24	0.28
33	-2.31	-0.24	-0.36
34	0.69	-0.40	0.78
35	1.28	2.12	-0.32
36	1.20	1.55	0.22
37	1.39	2.04	0.23
38	1.02	2.79	-0.53
39	-0.02	2.25	-0.91
40	-0.42	1.24	0.96
41	-2.35	1.17	0.86

* locality groups: 1-34, *S. secretus;* 35-40, *S. aquaticus;* 41, *S. lacustris.*

TABLE 5.10 Results of canonical variates analysis performed on total data set (41 groups) using five variables (the five shape variables).

Canonical variables		1	2	3
Eigen Values		3.59	1.25	1.04
Percentage Variance Explained		58.18	20.36	16.93
Eigen Vectors				
	V_2	-15.59	8.33	81.91
	V_3	-7.85	0.53	7.86
	V_4	-49.88	-5.54	-67.04
	V_5	44.21	-52.06	-25.25
	V_6	28.39	-5.96	15.52
Canonical Variate Means	*1	3.39	-0.06	-0.27
	2	0.35	0.26	1.38
	3	1.06	1.38	1.72
	4	-0.82	-0.55	1.38
	5	0.96	-0.84	0.17
	6	-0.25	2.14	2.15
	7	-2.33	1.33	1.12
	8	-0.74	-0.44	0.76
	9	-0.42	0.13	-0.20
	10	-3.10	0.20	-0.41
	11	0.01	-0.43	-0.10
	12	3.22	-1.47	0.81
	13	0.15	0.22	0.29
	14	0.67	0.57	0.27
	15	0.80	0.45	-0.71
	16	2.57	0.77	-0.49
	17	1.05	0.97	-1.20
	18	2.08	1.33	-1.80
	19	-0.01	-0.29	-0.22

TABLE 5.10 (continued)

Canonical Variate Means

20	-2.55	1.50	-0.91
21	0.21	0.64	0.94
22	0.10	0.15	0.56
23	-1.68	0.44	-0.84
24	-1.98	-0.93	-1.15
25	-0.21	0.05	-1.14
26	-0.83	0.14	-2.21
27	0.85	1.19	0.52
28	2.46	-0.56	-0.41
29	3.00	-2.64	-0.77
30	2.47	3.67	-0.98
31	-3.26	1.18	-0.06
32	-3.48	0.93	-0.49
33	2.03	-0.04	-0.32
34	-0.41	0.46	0.95
35	-1.74	-1.80	-0.36
36	-1.43	-1.30	0.35
37	-2.15	-1.42	-0.18
38	-1.47	-2.63	-0.23
39	0.00	-2.59	-0.06
40	0.10	-1.17	1.40
41	1.30	-0.99	0.77

* locality groups: 1-34, *S. secretus*; 35-40, *S. aquaticus*; 41, *S. lacustris*.

TABLE 5.11 Summary of the important features of the table of Mahalanobis distances (Table B-3) obtained for the canonical variate analysis on the total data set (41 groups) using six variables (one size and five shape variables).

Groups which are not significantly different in larval shape (Pairs of groups with M-distance <1.5)
1,16; 2,13; 2,21; 4,8; 4,34; 5,11; 5,19; 8,34; 8,36; 9,22; 9,25; 9,34; 10,31; 10,32; 11,19; 13,14; 13,21; 14,15; 14,21; 14,22; 14,27; 14,34; 15,17; 15,25; 17,18; 21,22; 21,27; 21,34; 22,34; 28,33; 31,32; 35,36
Groups which differ significantly from all others on the basis of larval shape
3; 6; 7; 12; 16; 20; 23; 24; 26; 29; 30; 37; 38; 39; 41

TABLE 5.12 Summary of the important features of the table of Mahalanobis distances (Table B-4) obtained for the canonical variate analysis on the total data set (41 groups) using five variables (the five shape variables).

Groups which are not significantly different in larval shape (Pairs of groups with M-distance <1.4)
1,16; 1,28; 2,13; 2,14; 2,21; 2,22; 2,34; 3,27; 4,8; 4,34; 4,40; 5,11; 5,19; 8,11; 8,22; 8,34; 8,36; 9,11; 9,19; 9,22; 9,25; 9,34; 10,32; 11,13; 11,14; 11,15; 11,19; 11,22; 11,25; 13,14; 13,19; 13,21; 13,22; 14,15; 14,19; 14,21; 14,22; 14,27; 14,34; 15,17; 15,19; 15,25; 17,18; 19,22; 19,25; 20,32; 21,22; 21,27; 21,34; 22,27; 22,34; 28,31; 28,32; 28,33; 31,32; 35,36; 35,37; 36,37
Groups which differ significantly from all others on the basis of larval shape
6; 7; 12; 16; 23; 24; 26; 29; 30; 38; 39; 41

To avoid repitition, only the implications of the canonical variate analysis performed on the five variable data set will be considered here and discussed in the following section (5.8). There are no fundamental differences between the results of the two analyses; however, the analysis based on shape variables alone is the more appropriate for discussion as shape is the factor of interest in this study. The results of the canonical variate analysis on the five variable data set are given in Figure 5.8.

Statistically, the importance of a canonical axis is given by the percentage of the total variation it accounts for. Table 5.10 shows that the first canonical axis accounts for 58% of the total variation, the second for 20% and the third for 16.9%. The first canonical axis is the largest, providing the greatest separation of groups and therefore must be considered to be the most statistically important. However, a smaller axis may be more important biologically. Blackith and Reyment (1971) note that the first canonical axis often represents some quantity which is numerically large but of limited consequence to the biologist. Often the first axis represents a size axis (Blackith and Reyment, 1971) as size is the character in which the greatest amount of variation is present. However, the fact that variables were transformed to adjust for size in this study suggests that the first axis here is reflecting variation in shape, rather than size.

As the first two axes account for a large proportion of the total variation then, as noted in Section 5.2, a graph of the first two axes plotted together may be considered as a fairly complete visual presentation of the similarities between groups. Examination of Figure 5.8 reveals that there is a continuous scatter of points along both the first and second axis and thus variation in shape within both *S. secretus* and *S. aquaticus* is largely of a continuous nature.

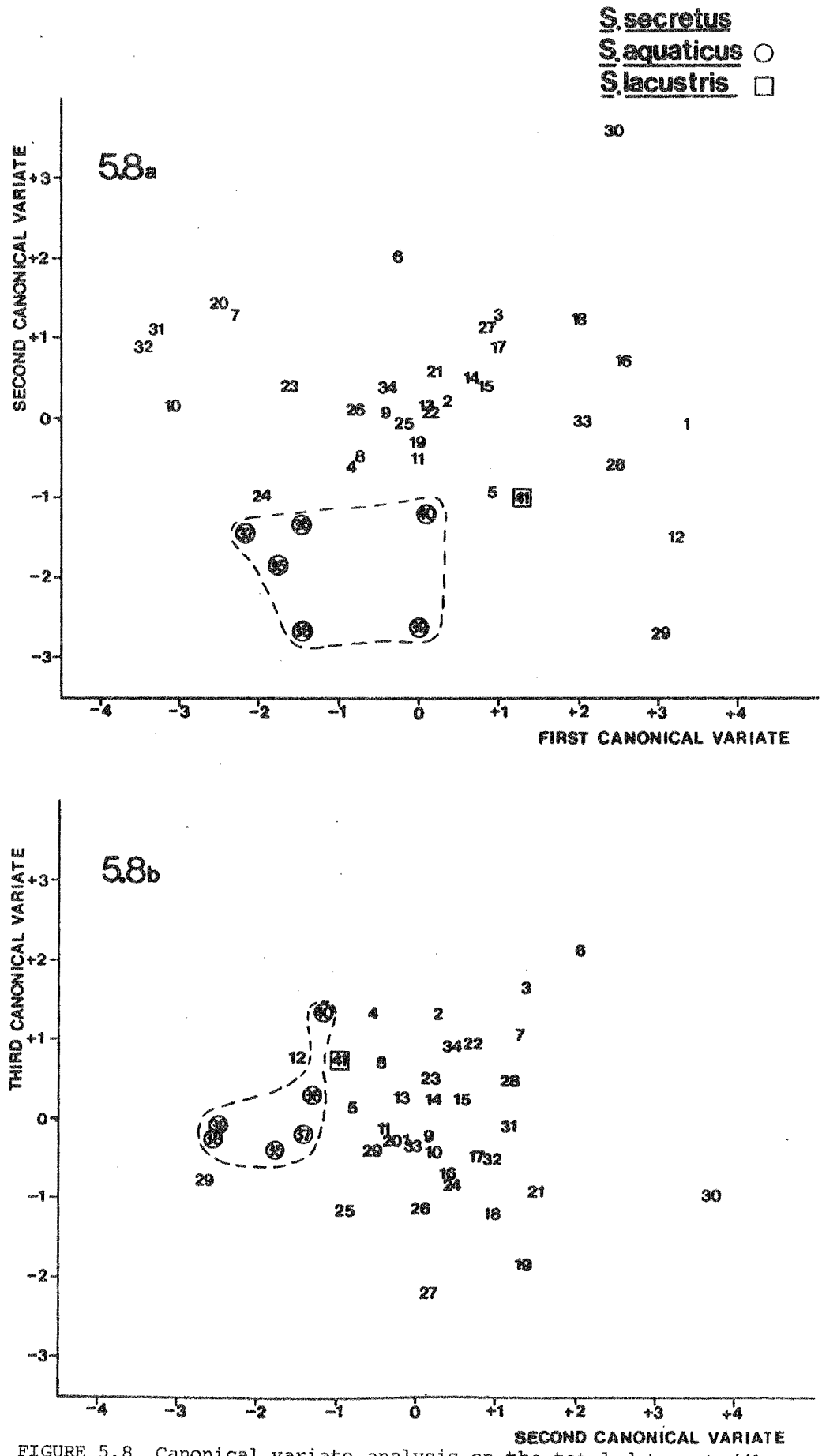


FIGURE 5.8 Canonical variate analysis on the total data set (41 groups), comprising 34 groups of *S. secretus* (1-34), six groups of *S. aquaticus* (35-40) and one group of *S. lacustris* (41), using five variables.
(a) first and second canonical variates plotted together.
(b) second and third canonical variates plotted together.
The five groups of *S. aquaticus* are enclosed within the dotted line.

The most accurate estimate of the distance between groups, however, is provided by the table of M-distances. Table 5.12 (the summary of the table of M-distances, Table B-4) shows that only nine of the 34 groups of *S. secretus*, two of the six groups of *S. aquaticus* and the single group of *S. lacustris* differ significantly from all others on the basis of shape. Table 5.12 also reveals that two groups of *S. aquaticus*, 36 and 40, are indistinguishable from two groups of *S. secretus*, 8 and 4, respectively. The scatter of groups on Figure 5.8a, however, shows groups 41 and 5 to be closer than 36 and 8 and 40 and 4. This anomaly arises from the fact that the third axis does play some part in indicating the separation of groups in the analysis and by considering the first and second axes only the effect of the third axis is ignored. This,in fact, provides an example of why the table of M-distances provides a more accurate estimation of distances between groups than the graph of first and second axes plotted together. The table of M-distances are based on the distances between groups on all three axes, not just the first two (as noted in Section 5.2).

The nature of larval shape changes along each axis is given by the relative magnitudes, and signs, of the eigen vectors (Table 5.10). In interpreting these values it must be remembered that the transformed variables; V_2, V_3, V_4, V_5 and V_6, correspond to the widths of segments 1, 3, 6, 9 and 12. On the first axis a decrease in the width of segments 1, 3 and 6 is accompanied by an increase in segments 9 and 12 and the greatest change occurs between segments 6 and 9. On the second axis segment 9 decreases markedly in respect to all other segments and this axis may well reflect the degree to which larvae are tapered posteriorly. No clear trends are evident on the third axis, a large increase in segment 1 is accompanied by a large decrease in segment 6, segments 9 and 12 also change in the opposite fashion.

To visualize the changes in larval shape predicted by the eigen

vectors representative larvae from six different groups at both the centre and ends of the first and second axes in Figure 5.8a were drawn (Figure 5.9). From Figure 5.9 it can be seen that the first axis represents a gradual change in larval shape from wide to narrow shields. A similar change occurs on the second axis from wide almost circular shields to narrow tapered shields. This axis clearly separates *S. secretus* from *S. aquaticus* on the basis of shape.

Canonical Variate Analysis on the Single Species *S. secretus*

The results of the canonical variate analysis on the *S. secretus* data set (34 groups) using six variables are given in Table 5.13 and the results of the analysis using five variables are given in Table 5.14. The tables of Mahalanobis distances for both analyses are given in Appendix B (Tables B-5 and B-6 respectively). Summaries of the important features of these tables are given in Tables 5.15 and 16 respectively. No major differences exist between the relative positions of groups under either analysis and therefore, as for the analysis conducted on the total data set, only the canonical variate analysis performed using five variables will be considered here.

The results of the canonical variate analysis on the five variable data set are plotted in Figure 5.10. Comparison of Figure 5.10 with Figure 5.8 (the graph of the canonical variate analysis on the total data set using five variables) reveals few differences in the relative distances between groups of *S. secretus* in either analysis.

From Table 5.14 it can be seen that the first axis accounts for 58% of the total variation, the second for 20% and the third for 16.9%. These results are identical to those obtained for the analysis on the total data set (Table 5.10). Table 5.16 (which summarises the table of Mahalanobis distances, Table B-6) shows that only nine of the 34 groups of *S. secretus* differ significantly from all others on the basis of larval

S. secretus: 6, 10, 9, 13, 1

S. aquaticus: 39

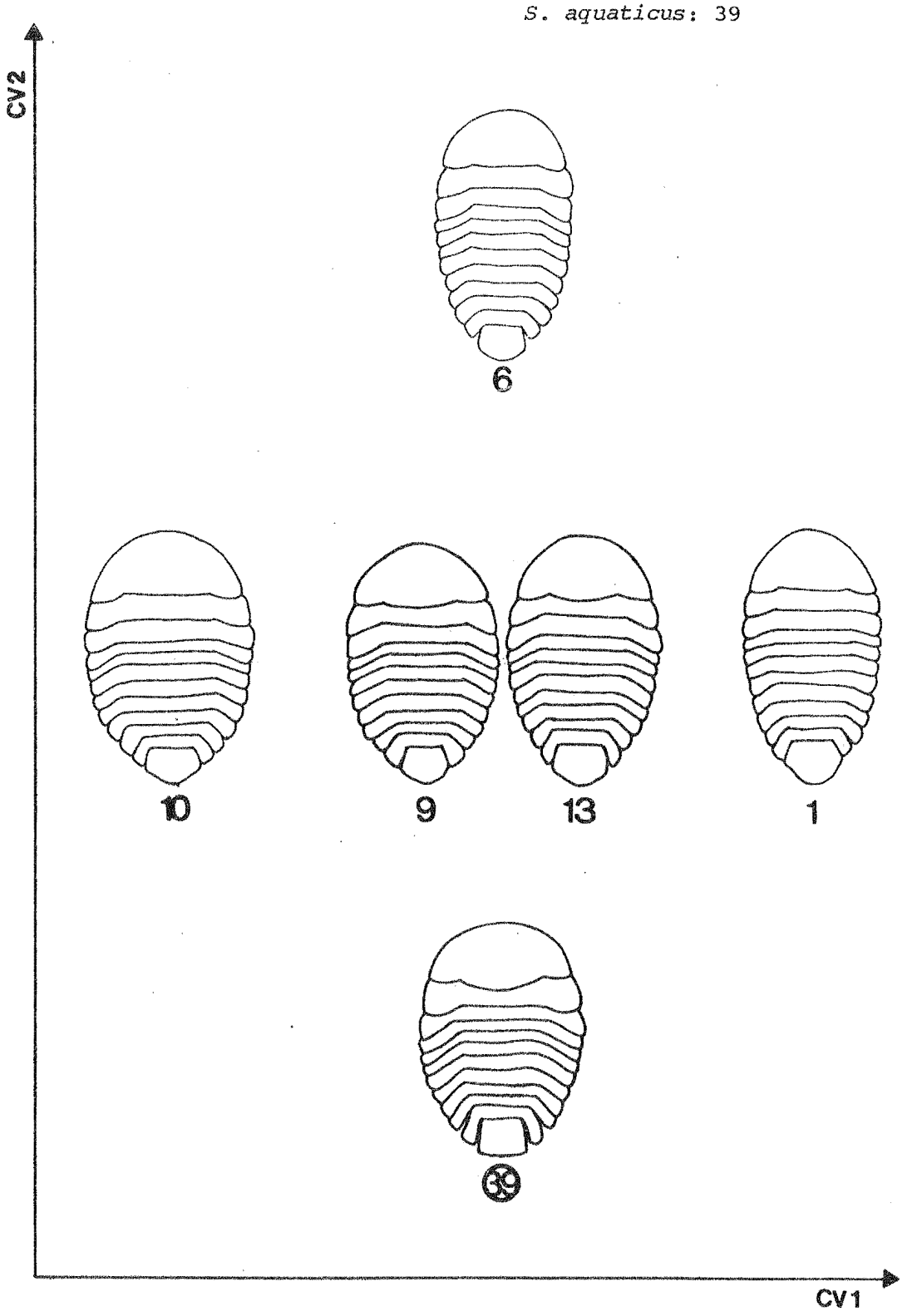


FIGURE 5.9 Trends in larval shape in *S. secretus* and *S. aquaticus* as determined by the distribution of groups on the first and second canonical axes in the canonical variates analysis on the total data set (41 groups) given in Figure 5.8a.

TABLE 5.13 Results of canonical variates analysis performed on *S. secretus* data set (34 groups) using six variables (one size and five shape variables).

Canonical Variables		1	2	3
Eigen Values		5.01	1.40	1.25
Percentage Variance Explained		58.45	16.33	14.61
Eigen Vectors	V_1	-6.60	5.75	1.03
	V_2	-20.12	49.22	24.68
	V_3	-5.17	2.03	1.70
	V_4	-55.78	-52.67	-20.92
	V_5	44.73	10.02	-53.28
	V_6	42.85	0.07	0.55
Canonical Variate Means	1	-2.65	-1.46	-0.34
	2	-0.59	1.38	-0.25
	3	-1.69	1.88	-1.51
	4	0.80	1.16	0.53
	5	-2.25	1.10	1.08
	6	0.92	1.58	-2.17
	7	3.05	1.07	-0.80
	8	0.97	0.58	0.59
	9	0.64	-0.10	0.35
	10	3.21	0.43	0.89
	11	-1.58	1.38	1.04
	12	-4.35	0.89	1.05
	13	-0.09	0.39	0.06
	14	-0.20	-0.11	-0.45
	15	-0.49	-0.74	-0.05
	16	-1.72	-1.45	-0.94
	17	-0.74	-1.10	-0.49
	18	-1.16	-2.22	-0.90

TABLE 5.13 (continued)

Canonical Variate Means

19	-1.79	1.52	0.99
20	3.46	-0.53	-0.34
21	-0.02	0.73	-0.55
22	0.86	-0.26	-0.11
23	2.98	-1.07	0.44
24	2.56	-0.92	1.82
25	0.35	-0.71	0.68
26	2.62	-2.89	0.69
27	-0.59	0.25	-1.13
28	-2.63	-0.60	0.54
29	-3.73	-0.83	2.43
30	-1.80	-1.21	-3.33
31	3.58	0.80	0.02
32	3.61	0.63	0.39
33	-2.25	-0.29	0.10
34	0.74	0.68	-0.33

TABLE 5.14 Results of canonical variates analysis performed on *S. secretus* data set (34 groups) using five variables (the five shape variables).

Canonical Variables		1	2	3
Eigen Values		3.59	1.25	1.04
Percentage Variance Explained		58.18	20.36	16.93
Eigen Vectors	V_2	-15.59	8.33	81.91
	V_3	-7.85	0.53	7.86
	V_4	-49.88	-5.54	-67.04
	V_5	44.21	-52.06	-25.25
	V_6	26.13	-0.47	13.39
Canonical Variates Means	1	-3.20	-0.08	-0.18
	2	-0.11	-0.61	1.35
	3	-0.57	-1.92	1.01
	4	0.82	0.18	1.59
	5	-0.99	0.80	0.72
	6	0.88	-2.54	1.25
	7	2.65	-1.03	0.73
	8	0.75	0.39	1.08
	9	0.50	0.37	-0.06
	10	3.08	0.83	-0.15
	11	-0.01	0.75	0.31
	12	-3.23	0.72	1.52
	13	0.00	-0.04	0.44
	14	-0.43	-0.44	0.16
	15	-0.63	0.13	-0.66
	16	-2.28	-0.61	-0.74
	17	-0.81	-0.17	-1.35
	18	-1.76	-0.32	-2.07
	19	0.03	0.69	0.13

TABLE 5.14 (continued)

Canonical Variates
Means

20	2.78	-0.13	-1.17
21	0.06	-0.74	0.74
22	0.05	-0.11	0.63
23	1.76	0.68	-0.58
24	1.74	2.00	-0.35
25	0.24	0.87	-0.78
26	0.77	1.36	-1.87
27	-0.48	-1.17	0.05
28	-2.40	0.62	-0.00
29	-3.36	2.49	0.53
30	-1.65	-2.86	-2.46
31	3.47	-0.08	-0.15
32	3.60	0.33	-0.43
33	-1.89	0.14	-0.08
34	0.62	-0.51	0.80

TABLE 5.15 Summary of the important features of the table of Mahalanobis distances (Table B-5) obtained for the canonical variate analysis on the *S. secretus* data set (34 groups) using six variables (one size and five shape variables).

Groups which are not significantly different in larval shape (Pairs of groups with M-distance <1.5)

1,16; 2,13; 2,21; 4,8; 4,34; 5,11; 5,19; 8,9; 8,22; 8,34; 9,14;
9,15; 9,25; 9,34; 10,31; 10,32; 13,14; 13,21; 14,15; 14,22; 14,27;
14,34; 15,17; 15,25; 17,18; 21,27; 21,34; 22,34; 28,33; 31,32

Groups which differ significantly from all others on the basis of larval shape

3;6;7;12;16;23;24;26;29;30

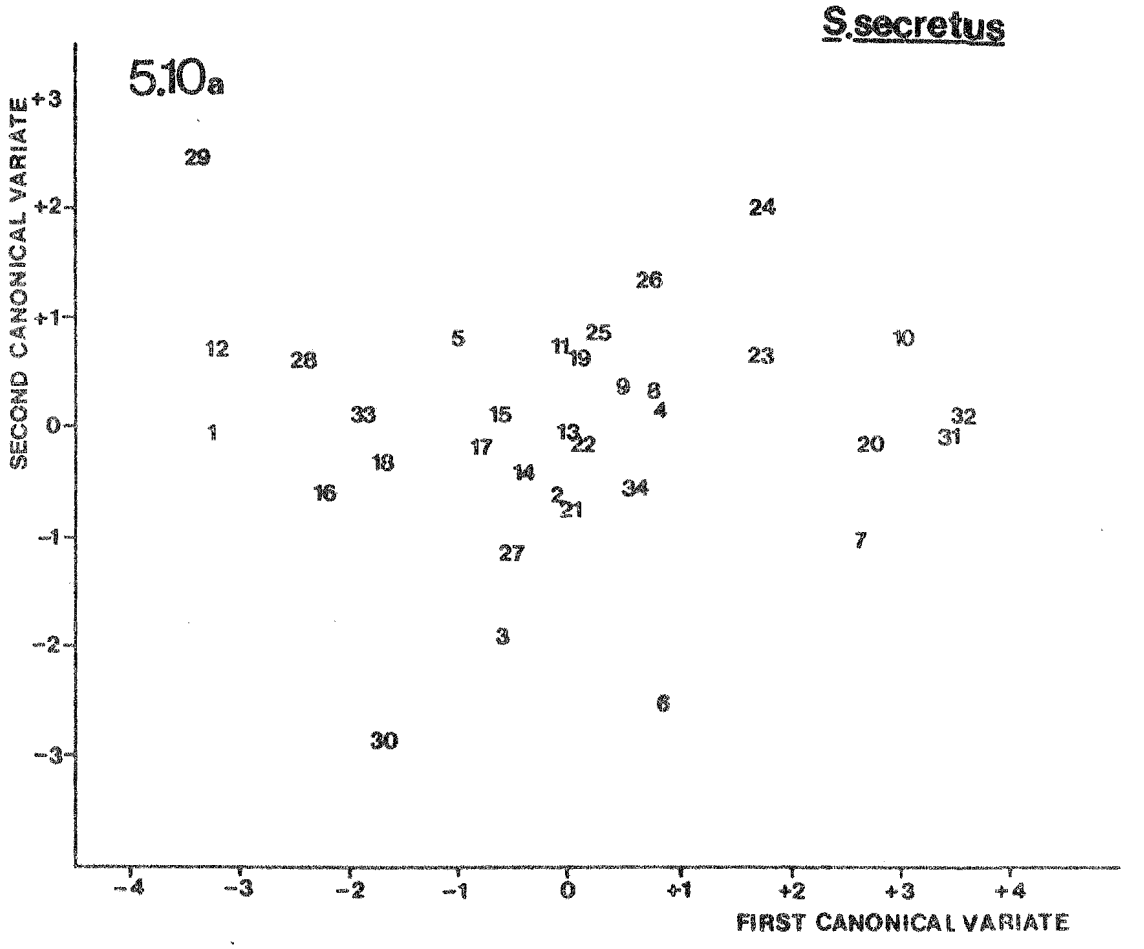
TABLE 5.16 Summary of the important features of the table of Mahalanobis distances (Table B-6) obtained for the canonical variate analysis on the *S. secretus* data set (34 groups) using five variables (the five shape variables).

Groups which are not significantly different in larval shape (Pairs of groups with M-distance <1.4)

1,16; 1,28; 2,13; 2,14; 2,21; 2,22; 2,34; 3,27; 4,8; 4,34; 5,11;
5,19; 8,11; 8,22; 8,34; 9,11; 9,19; 9,22; 9,25; 9,34; 10,32;
11,1; 11,3; 11,14; 11,15; 11,19; 11,22; 11,25; 13,14; 13,15;
13,19; 13,21; 13,22; 13,27; 14,15; 14,19; 14,21; 14,22; 14,27;
15,17; 15,19; 15,25; 17,18; 19,22; 19,25; 20,32; 21,22; 21,27;
21,34; 22,27; 22,34; 28,33; 31,32

Groups which differ significantly from all others on the basis of larval shape

6; 7; 12; 16; 23; 24; 26; 29; 30



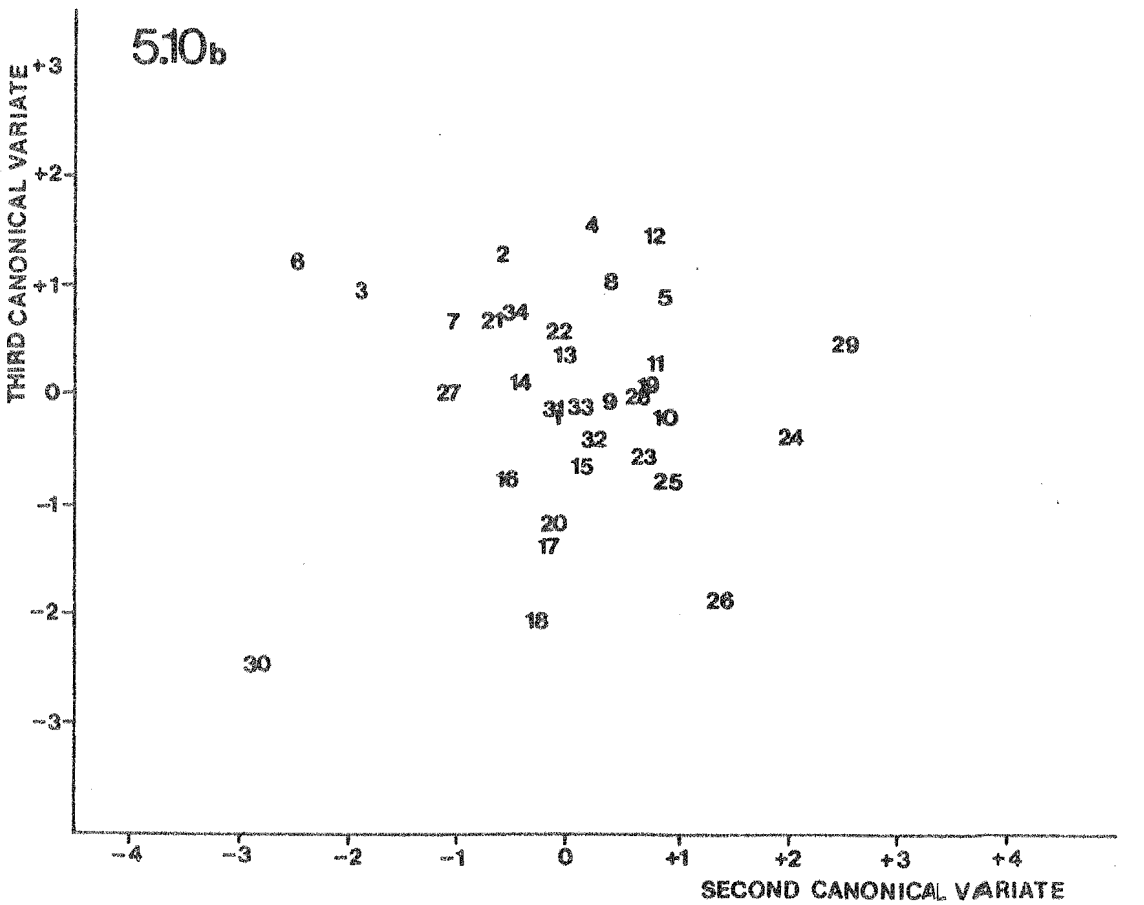


FIGURE 5.10 Canonical variate analysis on the *S. secretus* data set (34 groups, 1-34) using five variables.
(a) first and second canonical variates plotted together.
(b) second and third canonical variates plotted together.

shape. These nine groups (6, 7, 12, 16, 23, 24, 26, 29 and 30) were also found to be significantly different in the canonical variate analysis performed on the total data set (Table 5.12).

Comparison of the eigen vectors given in Tables 5.10 and 5.14 reveals that the same trends in shape seen in the analyses on the total data set of 41 groups also exist in the analysis of the 34 groups of *S. secretus* alone. The first axis reflects a comparative change in width between the anterior and posterior regions of the larval shield while the second axis reflects a marked change in the width of segment 9 with respect to all other segments. Representative larvae from five different groups at both the centre and ends of the first and second axes in Figure 5.10 are illustrated in Figure 5.11. The first axis reflects a change from narrow to wide shields and similarly the second axis reflects a change from narrow to wide shields.

A west-east trend in larval shape is evident in the groups scattered across the first axis in Figure 5.10a. Groups lying in the positive region of the first axis are predominantly from the west of Tasmania while those lying in the negative region are from the east. This west-east trend in larval shape is, in fact, a change from wide to narrow shields. All groups from high altitudes lie towards the centre of the first axis while lowland groups are well scattered across both areas. Therefore, while larval populations of *S. secretus* in high altitude streams exhibit similar shapes, populations in lowland streams may differ markedly.

Exactly the same trends in larval shape in *S. secretus* are evident under both the canonical variate analysis performed on the 34 groups of *S. secretus* alone and in the canonical variate analysis performed on the total data set of 41 groups which includes *S. aquaticus* (six groups) and *S. lacustris* (one group) as well as the 34 groups of *S. secretus*. To avoid repetition only the results of the canonical variate analysis

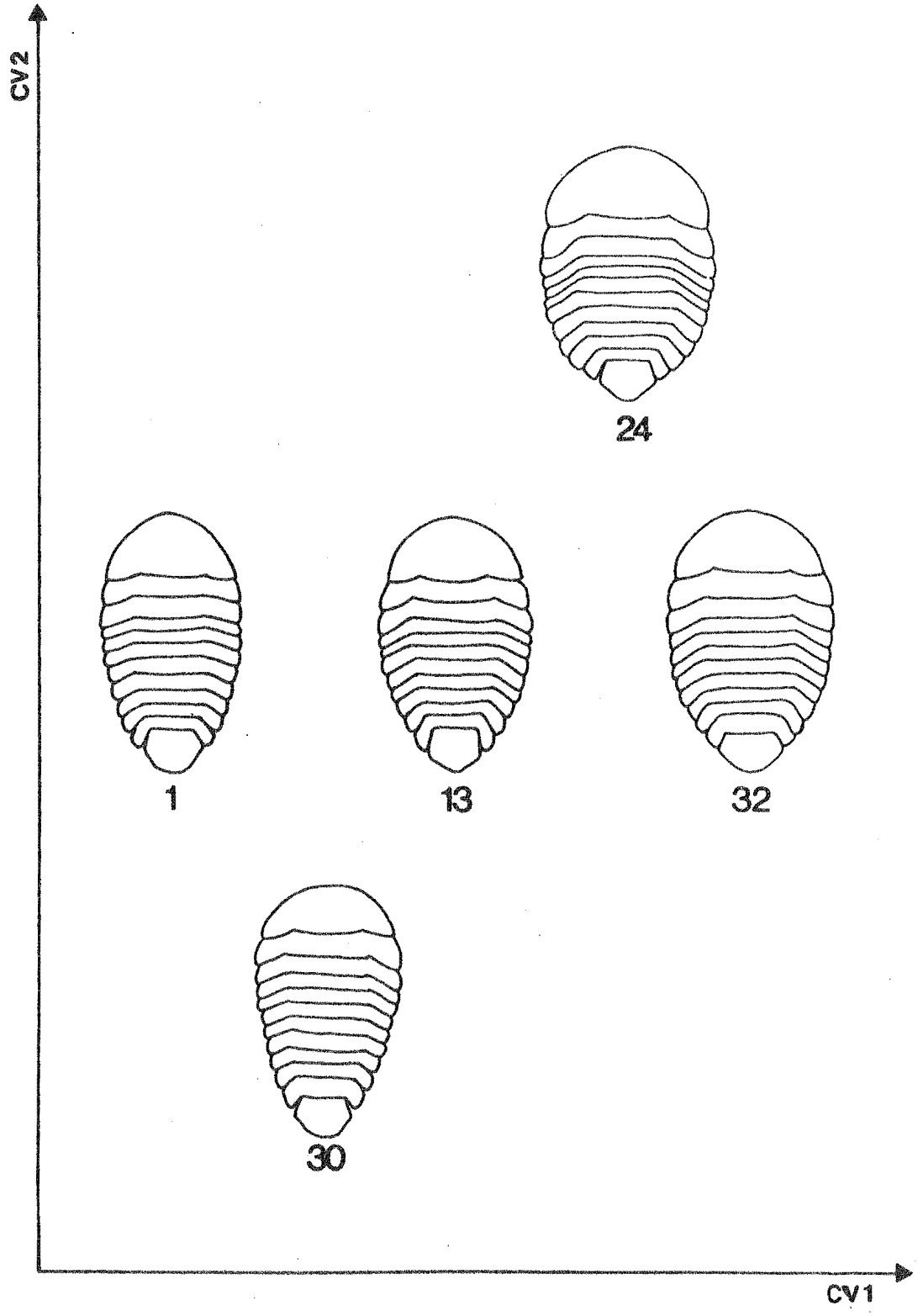


FIGURE 5.11 Trends in larval shape in *S. secretus* as determined by the distribution of groups on the first and second canonical axes in the canonical variate analysis on the *S. secretus* data set (34 groups) given in Figure 5.10.

performed on the total data set of 41 groups, using five variables, will be considered further here and discussed in the following section (5.6).

Testing for Sampling Error Using Two Groups from the Same Locality

The localities containing duplicate groups and the M-distances between each pair of groups (as given in Table B-4, Appendix B) are listed in Table 5.17 below.

TABLE 5.17 M-distances between pairs of groups from the same localities, as obtained from Table B-4 (Appendix B), the M-distances for the canonical variates analysis performed on the total data set of 41 localities using five variables.

Locality	Groups	M-distance between groups
Parsons Bay Creek	11, 19	0.21
Browns River	13, 14	1.04
Baxter Rivulet	15, 16	1.96*
Pearl Creek	17, 18	1.32
un-named Creek on the right bank on the Gordon River	31, 32	0.65

* The critical distance for the M-distance between pairs of groups in the five variable canonical variate analysis is 1.4 (calculated from the formula given in Section 5.2). The M-distance marked with an asterisk is the only one exceeding this critical distance.

From Table 5.17 (above) it can be seen that four of the five localities tested possessed pairs of groups of similar shape. For Baxter Rivulet however, the M-distance between the two groups indicated that they were significantly different, that is, they possessed larvae of different shapes.

To analyse differences between the two Baxter Rivulet groups a univariate analysis of variance was performed, between the two groups, on each variable. The F-ratios, and their probabilities, obtained in

these analyses are given in Table 5.18.

TABLE 5.18 F-ratios and probabilities for the univariate analysis of variances performed on the two Baxter Rivulet groups (15, 16) to compare individual variables.

	Variable*					
	V_1	V_2	V_3	V_4	V_5	V_6
F-ratio DF = 1,29	2.972	7.734	9.185	11.43	3.468	0.0065
Probability	0.095	0.009***	0.005***	0.002***	0.073	0.936

* Variables V_1 - V_6 represent the transformed variables defined in Section 5.6

From Table 5.18 (above) it can be seen that larvae in the two groups differ significantly with respect to three variables; V_2, V_3 and V_4. These variables correspond to the widths of three segments; segment 1, segment 3 and segment 6, respectively.

The reasons why the two groups taken from the same locality, Baxter Rivulet, differ in shape are not clear. Further analysis of shape variation within this locality, based on measurement of a large number of larvae, is needed. Although the duplicate groups in the four other localities tested were all similar in shape this difference in the Baxter Rivulet groups suggests that the entire analysis must not be regarded as wholly conclusive. A more extensive analysis of larval shape variation within localities is still needed.

Testing Measurement Error

The M-distance between the two groups, 21 and 34, obtained from the measuring the same set of 15 larvae from Myrtle Forest Creek twice, was 0.77 (from Table B-4, the M-distances obtained for the canonical variate analysis performed on the total data set of 41 groups using five variables). As stated above, the critical M-distance denoting a real

separation between groups was 1.4 for the five variable analysis. The M-distance of 0.77 is below this value and thus the two groups are indistinguishable on the basis of shape. This suggests, as would be hoped, that measurement error was not playing a significant role in distinguishing groups.

Testing for Distinct Subgroups within Each Group

The dendrograms obtained for the cluster analyses performed on the 41 groups in the total data set are given in Figure 5.12. As noted previously (Section 5.6) the cluster analyses, and the dendrograms produced, are of little value in isolation but enable some comparisons to be made between groups.

Differences between dendrograms 21 and 34, the two Myrtle Forest Creek groups representing the same group of 15 larvae measured twice, illustrate the differences in clustering that can occur where only slight differences in measurement exist.

Differences between the dendrograms obtained for localities where two groups of larvae were measured, Parson's Bay Creek (11 and 19), Browns River (13 and 14), Pearl Creek (17 and 18) and an un-named creek on the right bank of the Gordon River (31 and 32) illustrate the differences in clustering that can occur between two groups of larvae from the same population. Greater differences were evident between the two groups (15 and 16) from Baxter Rivulet and this was to be expected as the M-distance given in Table 5.17 above had indicated that the two groups were significantly different in larval shape.

It is interesting to note that both lacustrine groups, 30 and 41, *S. secretus* from Lake Pedder and *S. lacustris* from Lake Sorell, respectively, exhibit similar, and extremely low, variabilities in larval shape within each group. Possibly some factor (or factors) is more constant in the lacustrine environment than in the riverine one, resulting in

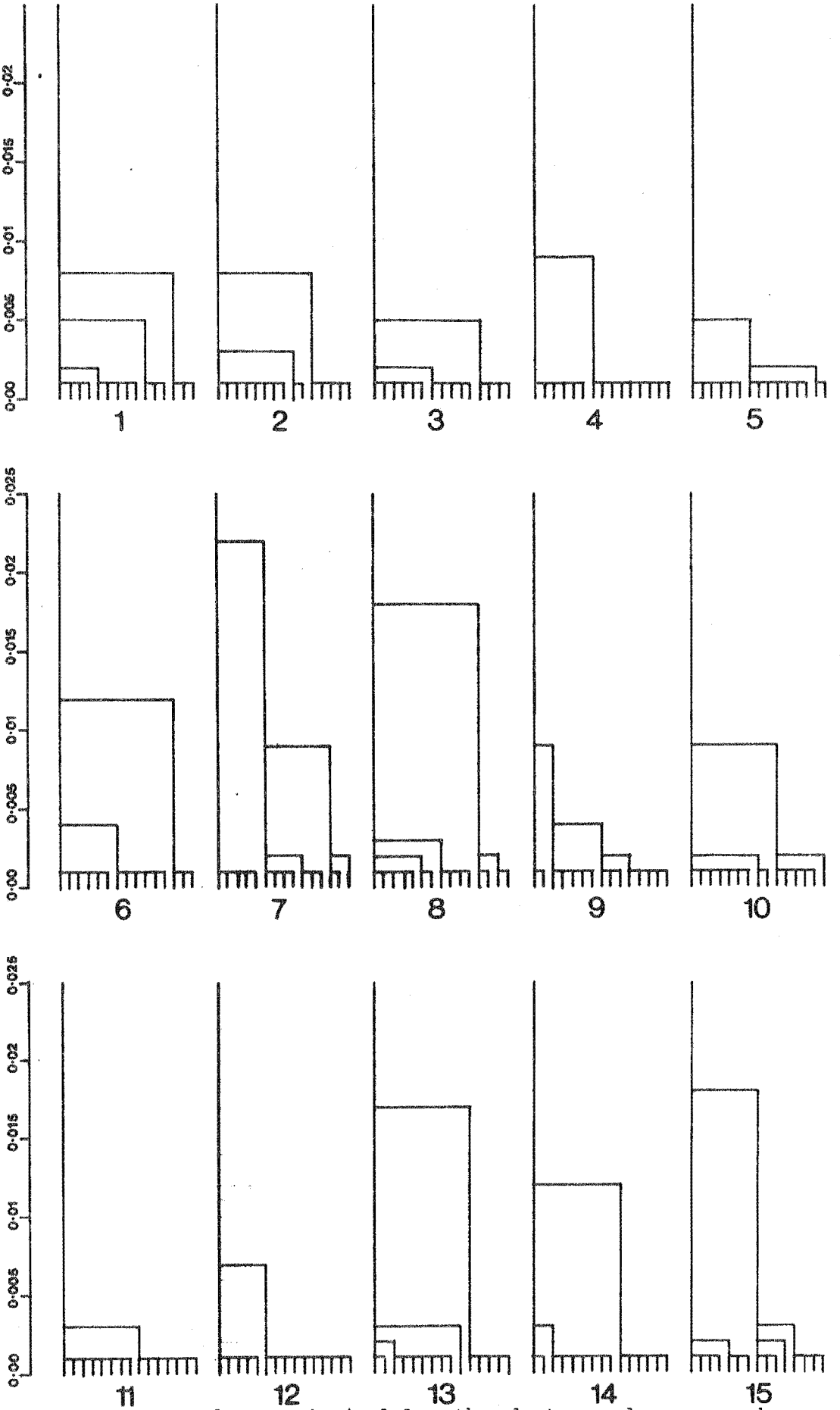


FIGURE 5.12 Dendograms obtained from the cluster analyses on each group (41) in the total data set comprising 34 groups of *S. secretus* (1-34), six groups of *S. aquaticus* (35-40) and one group of *S. lacustris* (41). Each group is represented by one dendogram and each larva within a group (15) is represented by one of the 15 lowest divisions.

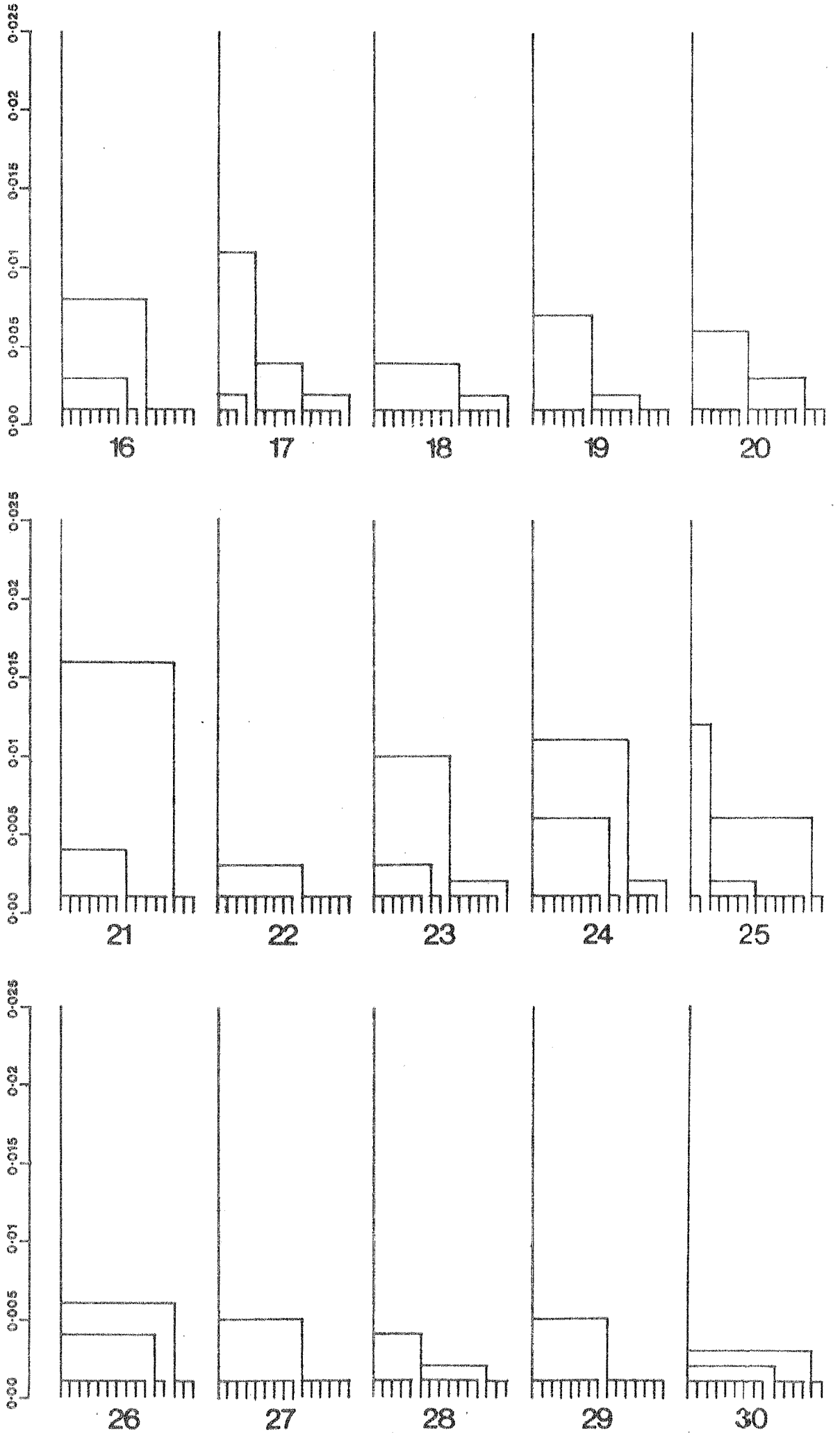


FIGURE 5.12 (cont'd)

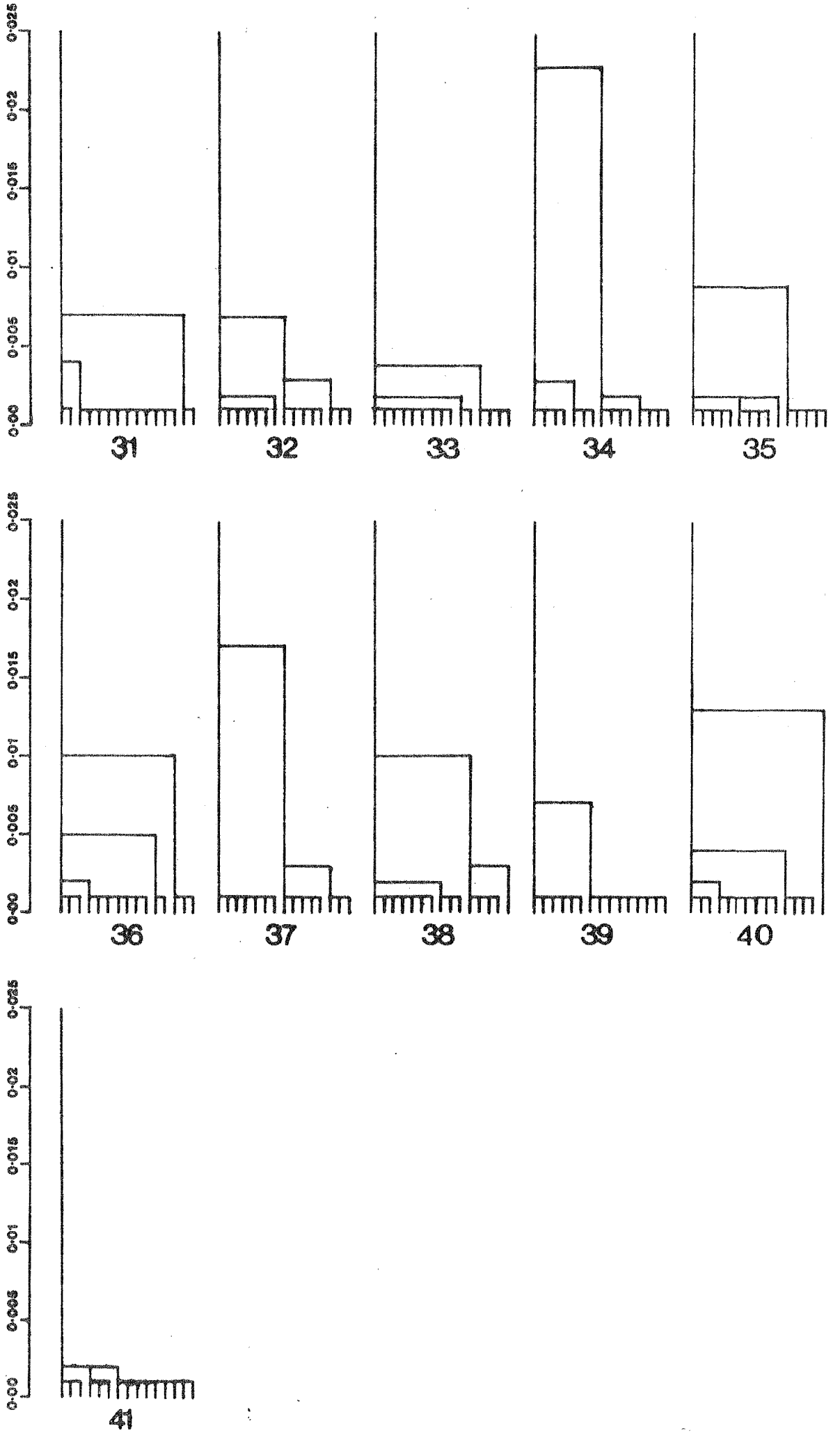


Figure 5.12 (cont'd)

greater uniformity in larval shape in the former environment.

From the differences in clustering in the groups cited above it would be unwise to place too much emphasis on the individual group results of this cluster analysis. The overall result of this cluster analysis is that two or more distinct and well separate subgroups are not present within groups. This suggests that variability within groups is of a continuous rather than a discrete nature.

The variances obtained in the one-way analysis of variance performed on each variable over the 41 groups in the final data set are given in Table 5.19. The variances are all low and not significant at either the 5% or 1% levels. This result supports that obtained in the cluster analysis, that two distinct and well-separated subgroups are not present within groups.

Correlations Between Canonical Variate Means and Environmental Variables

Correlation coefficients (r) between the mean scores on each of the three canonical axes (listed in Table 5.10) and ten continuous environmental variables (listed in Table 5.8) are given in Table 5.20. This table also gives correlations between the different environmental variables and thus provides an indication of the way in which these variables are interrelated. The two-way contingency tables constructed to examine the relationship between substratum and the three canonical axes are given in Table 5.21.

Stream Order

The highest correlations between canonical and environmental variables (Table 5.20) exists between the second canonical axis and both stream order ($r = 0.83$) and the number of tributaries ($r = 0.75$). As stream order and the number of tributaries are also highly correlated

TABLE 5.19 Variances obtained from the analysis of variance on each variable in each group for the total data set (41 groups). In all cases the degrees of freedom are: 1,14.

Group* (Locality Number)	Variances**					
	V_1	V_2	V_3	V_4	V_5	V_6
1	0.05716	0.00062	0.00068	0.00055	0.00026	0.00074
2	0.00638	0.00051	0.00054	0.00043	0.00035	0.00052
3	0.00368	0.00017	0.00032	0.00028	0.00022	0.00040
4	0.01109	0.00034	0.00041	0.00040	0.00033	0.00077
5	0.01072	0.00027	0.00034	0.00030	0.00021	0.00047
6	0.01594	0.00080	0.00078	0.00056	0.00035	0.00039
7	0.01278	0.00135	0.00143	0.00122	0.00087	0.00125
8	0.01262	0.00093	0.00095	0.00097	0.00074	0.00074
9	0.01717	0.00078	0.00074	0.00032	0.00032	0.00136
10	0.01766	0.00037	0.00065	0.00050	0.00042	0.00096
11	0.01073	0.00015	0.00013	0.00021	0.00029	0.00031
12	0.01978	0.00031	0.00037	0.00028	0.00031	0.00057
13	0.00549	0.00064	0.00067	0.00058	0.00051	0.00053
14	0.00906	0.00057	0.00085	0.00050	0.00043	0.00115
15	0.01994	0.00112	0.00094	0.00085	0.00067	0.00108
16	0.03202	0.00044	0.00044	0.00058	0.00041	0.00093
17	0.00647	0.00074	0.00086	0.00059	0.00073	0.00076
18	0.01855	0.00051	0.00020	0.00015	0.00018	0.00069
19	0.02028	0.00264	0.00226	0.00201	0.00149	0.00196
20	0.00815	0.00018	0.00037	0.00048	0.00030	0.00033
21	0.01560	0.00022	0.00033	0.00031	0.00040	0.00075
22	0.00615	0.00078	0.00091	0.00068	0.00064	0.00082
23	0.02495	0.00020	0.00015	0.00008	0.00017	0.00061
24	0.02263	0.00056	0.00071	0.00088	0.00065	0.00063
25	0.01430	0.00118	0.00092	0.00071	0.00028	0.00088
26	0.02646	0.00037	0.00051	0.00041	0.00038	0.00111
27	0.01771	0.00021	0.00026	0.00021	0.00021	0.00054
28	0.02127	0.00019	0.00031	0.00028	0.00025	0.00058
29	0.02253	0.00030	0.00028	0.00017	0.00029	0.00105
30	0.01124	0.00016	0.00015	0.00016	0.00032	0.00062
31	0.01210	0.00044	0.00055	0.00041	0.00035	0.00078
32	0.00713	0.00046	0.00044	0.00039	0.00034	0.00046
33	0.00417	0.00025	0.00023	0.00023	0.00022	0.00038
34	0.00596	0.00095	0.00133	0.00096	0.00072	0.00249
35	0.02154	0.00054	0.00052	0.00035	0.00046	0.00095
36	0.04925	0.00071	0.00070	0.00044	0.00061	0.00100
37	0.02769	0.00086	0.00077	0.00089	0.00074	0.00128
38	0.00936	0.00068	0.00060	0.00035	0.00049	0.00054
39	0.07114	0.00030	0.00034	0.00029	0.00029	0.00130
40	0.02878	0.00065	0.00074	0.00065	0.00052	0.00087
41	0.00854	0.00010	0.00012	0.00016	0.00025	0.00026

* Groups: 1-34, *S. secretus*; 35-40, *S. aquaticus*; 41, *S. lacustris*

** V_1 - V_6 are the transformed variables (as described in Section 5.6)

TABLE 5.20 Correlations between canonical variables and environmental variables for the 41 groups in the final study.
C_1, C_2 and C_3 are the canonical variable means, in the canonical variate analysis on the total data set (41 groups) using five variables, as listed in Table 5.10.
E_1-E_{10} are the environmental variables as listed in Table 5.8.

Variables	Correlation coefficient, r	Variables	Correlation coefficient, r	Variables	Correlation coefficient, r
C_1 E_1	-0.10	C_2 E_1	0.83*	C_3 E_1	0.02
C_1 E_2	-0.05	C_2 E_2	0.75*	C_3 E_2	-0.02
C_1 E_3	-0.28	C_2 E_3	0.44	C_3 E_3	-0.24
C_1 E_4	-0.09	C_2 E_4	-0.34	C_3 E_4	0.42
C_1 E_5	0.63*	C_2 E_5	-0.49	C_3 E_5	-0.22
C_1 E_6	-0.55*	C_2 E_6	0.49	C_3 E_6	0.24
C_1 E_7	-0.24	C_2 E_7	0.05	C_3 E_7	0.21
C_1 E_8	0.23	C_2 E_8	0.01	C_3 E_8	-0.28
C_1 E_9	-0.01	C_2 E_9	0.26	C_3 E_9	-0.36
C_1 E_{10}	-0.01	C_2 E_{10}	0.09	C_3 E_{10}	-0.28
E_1 E_2	0.92	E_2 E_3	0.59	E_3 E_4	-0.24
E_1 E_3	0.51	E_2 E_4	-0.29	E_3 E_5	-0.27
E_1 E_4	-0.37	E_2 E_5	-0.29	E_3 E_6	0.40
E_1 E_5	-0.36	E_2 E_6	0.34	E_3 E_7	0.20
E_1 E_6	0.39	E_2 E_7	-0.05	E_3 E_8	0.11
E_1 E_7	-0.08	E_2 E_8	-0.04	E_3 E_9	0.25
E_1 E_8	0.02	E_2 E_9	0.16	E_3 E_{10}	0.28
E_1 E_9	0.20	E_2 E_{10}	0.09		
E_1 E_{10}	0.11				
E_4 E_5	-0.11	E_5 E_6	-0.78	E_6 E_7	0.05
E_4 E_6	0.08	E_5 E_7	-0.56	E_6 E_8	-0.36
E_4 E_7	0.24	E_5 E_8	0.36	E_6 E_9	0.05
E_4 E_8	-0.74	E_5 E_9	-0.47	E_6 E_{10}	0.04
E_4 E_9	-0.79	E_5 E_{10}	-0.07		
E_4 E_{10}	-0.7				
E_7 E_8	-0.22	E_8 E_9	0.70	E_9 E_{10}	0.77
E_7 E_9	0.04	E_8 E_{10}	0.64		
E_7 E_{10}	0.12				

* The asterisk marks the highest correlations obtained between canonical variate means and environmental variables.

TABLE 5.21 Contingency tables constructed to test the hypothesis that there is no relationship between substrate and the three canonical variates.

		Substrate			
		Quartzite	Alluvials	Dolerite	
First canonical axis	+	1(16.1)	4(3.9)	18(12.9)	23
	-	10(4.8)	3(2.3)	5(10.9)	18
		11	7	23	41

$\chi^2_{(D.F.=2)} = 14.65$, $P<0.001^{***}$

		Substrate			
		Quartzite	Alluvials	Dolerite	
First canonical axis	+	8(5.9)	6(3.8)	8(12.3)	22
	-	3(5.1)	1(3.2)	15(10.6)	19
		11	7	23	41

$\chi^2_{(D.F.=2)} = 7.84$, $0.02<P<0.01^{**}$

		Substrate			
		Quartzite	Alluvials	Dolerite	
First canonical axis	+	3(4.8)	3(3.1)	12(10.1)	18
	-	8(6.2)	4(3.9)	11(12.9)	23
		11	7	23	41

$\chi^2_{(D.F.=2)} = 1.82$, not significant

($r = 0.92$) only the relationship between the former and larval shield shape will be considered further.

This correlation indicates that most of the localities present in the negative region of the second canonical axis (Figure 5.8a) are of high stream order while those in the positive region are of low stream order; that is, larvae of wide, almost circular shields are present in streams of high stream order (larger streams or rivers) while those with narrow, tapered shields are in streams of low order (small streams). Most localities in the former region contain *S. aquaticus* and this agrees well with field observations. This species appears to be restricted to larger streams and rivers (Chapter 4) and is usually very wide, almost circular, in shape.

Where *S. secretus* occurs in high order streams larval shields are usually wide. However, within first order streams *S. secretus* exhibits a range of shapes. Larvae in first order streams in the east of Tasmania are narrow-elongate to moderately wide and tapered while larvae in first order streams on the west coast are moderately wide to very wide. Narrow-elongate forms of *S. secretus* are never found in high order streams, that is, larger streams and rivers.

Stream order *per se* cannot influence the expression of larval shape but rather reflects the influence that various factors associated with streams of different signs may have. Abell (1961) suggests that stream order, as well as some of the other physiographic concepts of drainage analysis, enable biologists to describe stream systems accurately and consistently. Hynes (1970) also notes that the concept of stream order may be of considerable value in biological studies as a useful method of stream classification.

Climatic Factors

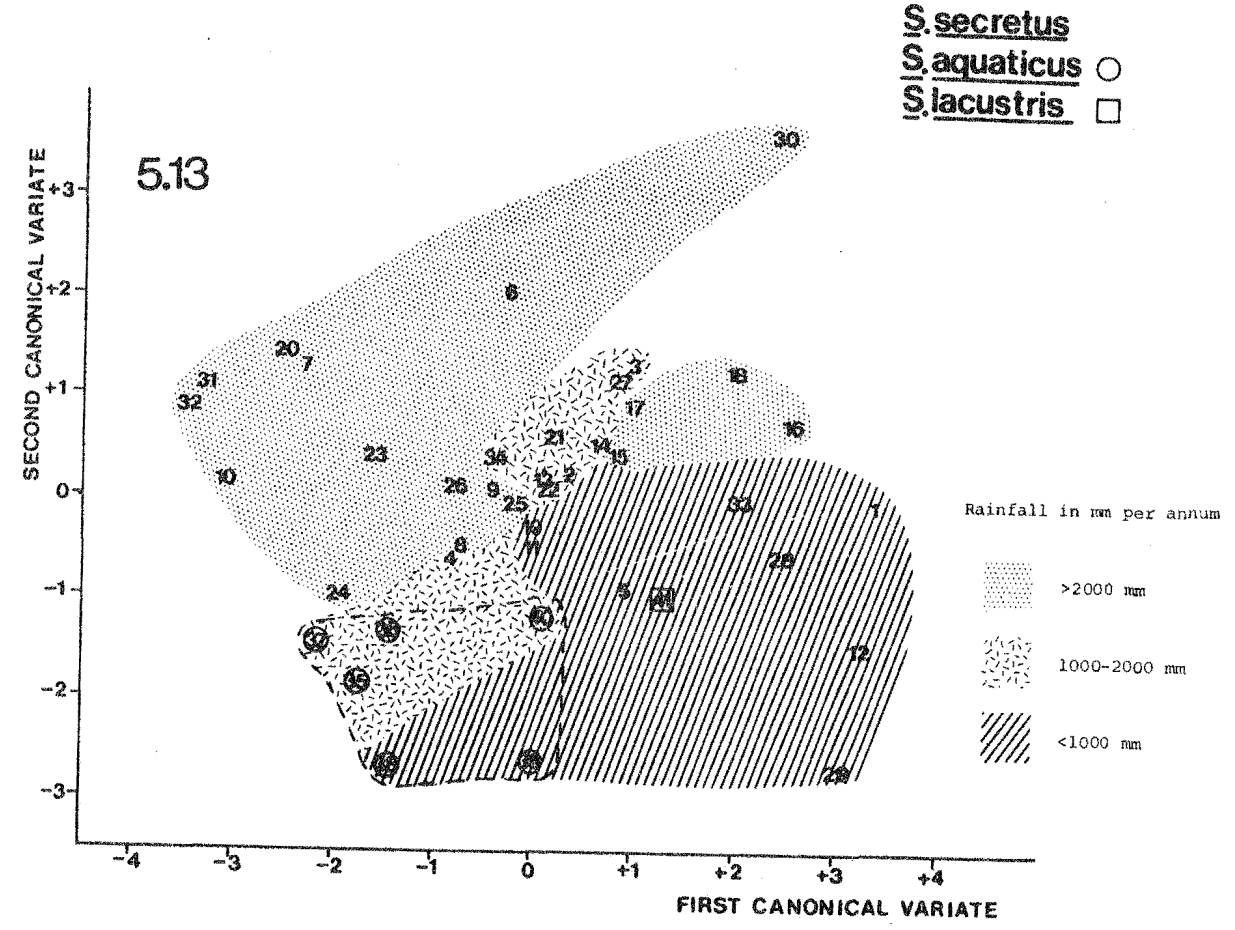
The west-east trend in larval shield shape, noted above, may well be

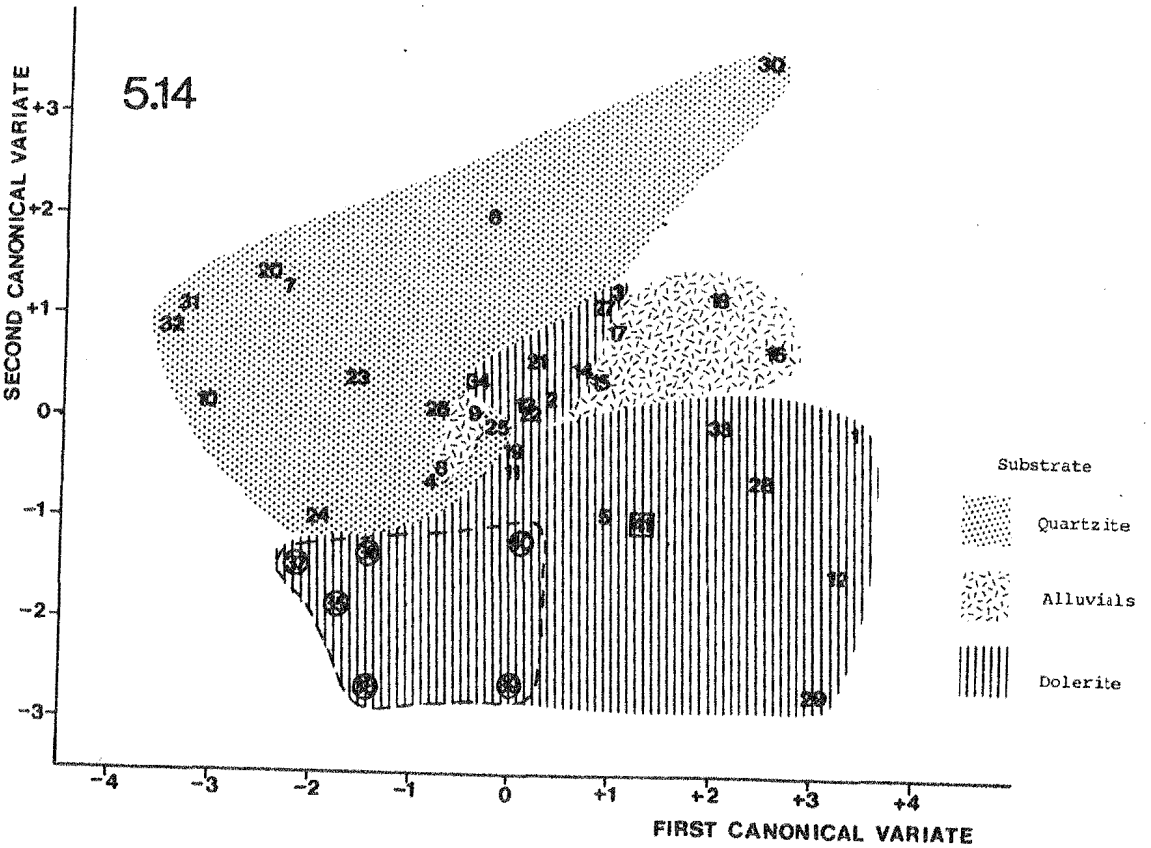
a result of the marked west-east variation of climate, and especially rainfall, that exists in Tasmania as a result of the combined effect of the prevailing westerly winds and the mountainous terrain of the western half of the State (Bureau of Meteorology, 1979). Because of the topography there is a strong gradation of rainfall from west to east, illustrated in Figure 5.8, with a distinct rain shadow east of the Central Plateau. Rainfall and rainfall variability are strongly negatively correlated (Table 5.20) and the rainfall on the east coast of Tasmania is more than twice as variable as that on the west (Watson and Wylie, 1972).

Daytime temperatures in the west of Tasmania are generally lower than those in the east due to greater cloud cover over the western half as a result of persistent westerlies. Temperatures in the east are further increased by the Föhn effect which warms and dries westerly airstreams as they descend to the Midlands, the east coast and south east districts (Bureau of Meteorology, 1979).

The first canonical axis only is correlated with both rainfall ($r = 0.63$) and rainfall variability ($r = -0.55$) (Table 5.2). The relationships between rainfall distribution and the distribution of groups according to shape, in the canonical variate analysis, is presented visually in Figure 5.13 and Plates 5.1 and 5.2. Maximum correlation between rainfall distribution and the shape of larvae appears to occur along an axis at 45° to the first canonical axis.

Although there are some exceptions, larvae of *S. secretus* with wide, almost circular shields occur in the highest rainfall region (>2000 mm per annum), larvae with moderately wide shields occur in all three rainfall regions but predominate in the intermediate zone (1000-2000 mm per annum) while larvae with narrow elongate shields occur in the lowest rainfall region (<1000 mm per annum). The greatest variations in shape between populations occurs between groups of *S. secretus* in the high





FIGURES 5.13-5.14 (5.13) The relationship between rainfall regimes and larval shape and; (5.14) the relationship between substrate and larval shape. In both cases larval shape is represented by the distribution of groups in the canonical variate analysis on the total data set (41 groups) using five variables (Figure 5.8a).

rainfall regions. This is most clearly illustrated in Plate 5.1. *S. aquaticus* occurs in both the low (<1000 mm per annum) and intermediate (1000-2000 per annum) rainfall regions.

Rainfall and rainfall variability do not influence the expression of larval shape directly, but rather, indirectly as a result of their effect on other stream parameters including depth and velocity. Both the amount of rainfall and its frequency over the year will affect depth and mean velocities (and as a consequence, stream temperatures) more markedly in first order streams than higher order streams.

No correlations were obtained between the canonical variate axes and temperature (Table 5.20); however, as noted in Section 5.6 , it is possible that the temperature data used here do not truly reflect the temperature regimes experienced by larvae. Comparison of Figures 5.6 and 5.7, the graphs of weekly temperature maxima and minima in Lambert Creek and Browns River, two localities included in the analysis, reveals the differences in both absolute temperature and the temperature range that can occur between high altitude and low altitude groups included in the analysis. These sites represent high and low altitude populations on the slopes of Mt. Wellington in the south-east of Tasmania. All high altitude groups from this region are clustered around the origin on the canonical axis while the low altitude groups from the same region are spread further across the positive region of this same axis (Figure 5.8a).

Once again it is not altitude *per se*, but rather altitude-linked environmental factors such as temperature or water velocity, that may be influencing the expression of larval shapes. These results suggest that some factor (or factors) in the environment of high altitude streams is constant, producing larvae of similar shape, regardless of geographical location; however, the same constancy of shape was not seen between populations in lowland streams possibly because that factor is more variable in lowland streams or other factors are also acting to influence the

expression of larval shape.

Substratum

The two-way contingency tests applied to the three canonical variate axes and the three categories of substrate (Table 5.21) reveal significant relationships between substrate and both the first and second canonical axes. That is, a relationship exists between the substrate and the occurrence of different larval shapes as indicated by the position of groups on the first and second axes.

The relationship between the different substrates and the distribution of groups in the canonical variate analysis is presented visually in Figure 5.14 and, together with rainfall, in Plate 5.2. Comparison of Figures 5.13 and 5.14 reveals that the relationship between substrate and larval shape is very similar to that between rainfall and larval shape and it is therefore difficult to separate the effects of either factor .

A west-east trend is again present because the quartzitic localities are most common in the west of Tasmania and doleritic localities in the east. Maximum association of substratum with larval shape appears to occur along an axis orientated at 45° to the first axis.

The widest, almost circular forms of *S. secretus* occur on quartzite. Larvae of moderately wide, tapered form occur on all three substrates while, with two exceptions (Lake Pedder and the Little Donaldson River tributary), the narrowest larvae occur on dolerite. *S. aquaticus* occurs only on dolerite.

The classification of substratum into three categories denoting rock type is, however, probably far too crude a parameter to reveal the true nature of the effect of the substratum on larval shape. Data on both the size and arrangement of rocks on the stream bed (bed roughness) and the surface roughness of the different rock types are now required.

Three Dimensional Graphs, Rainfall and Substrate

Plates 5.1 and 5.2 show the three dimensional graphs constructed for both the canonical variate analysis performed on the total data set of 41 groups (34 groups of *S. secretus*, six of *S. aquaticus* and one of *S. lacustris*) and the analysis performed on the 34 groups of *S. secretus* alone.

As stated in Section 5.6 the three planes (x, y and z) represent the three canonical axes (first, second and third, respectively) and the beads on the end of each rod denote the mean position of a group as determined by larval shape. Different colour beads were used to denote both the rainfall regime of each group (locality) (Plates 5.1 and 5.2) and the substratum (Plate 5.1).

For simplicity three rainfall regimes were designated; localities receiving 2000 mm per year, or more, were represented by blue beads, 1000-2000 mm per year by green beads, and less than 1000 mm per year, by orange beads. In Plate 5.1 the lower beads denote rainfall while the upper beads denote substratum. Quartzite was represented by blue beads, dolerite by orange beads and alluvials (sandstones, mudstones and shales) by yellow beads. The six rods marked with pink beads, mid-way, denote groups of *S. aquaticus*. In Plate 5.2 the beads denoting rainfall, only, are used and all groups are *S. secretus*.

Three dimensional graphs enable the distances between groups, as determined by the canonical variate analysis to be seen at once, rather than estimated from a consideration of their positions on axes, taken in pairs, as given in Figures 5.8 and 5.10. For both plates the graphs have been photographed from the orientation which gives the clearest separation of groups, in this case, a diagonal one. The ability to view plots easily, in different orientations, is an advantage of the three-dimentional graph. A disadvantage is the visual accentuation

PLATE 5.1 Three dimensional graph of the canonical variate analysis on the total data set of 41 groups showing the relationship between rainfall, substrate and larval shape (indicated by the relative positions of groups in the analysis). Each group is represented by the upper most bead on each rod. The three canonical axes (1, 2 and 3) are in the three planes (x, y and z). The colours of the upper beads denote substrates; quartzite (blue), alluvials (yellow) and dolerite (orange). The colours of the lower beads denote rainfall regimes; >2000 mm per annum (blue), 1000-2000 mm per annum (green) and <1000 mm per annum (orange). Groups of *S. aquaticus* are marked with pink beads midway along rods.

PLATE 5.2 Three dimensional graph of the canonical variate analysis on the *S. secretus* data set (34 groups) showing the relationship between rainfall and larval shape (indicated by the relative positions of groups in the analysis). Each group is represented by a bead. The three canonical axes are in the three planes x, y and z. The colours of the beads denote rainfall regimes as described for the lower beads in Plate 5.1 (see above).

Plate 5.1

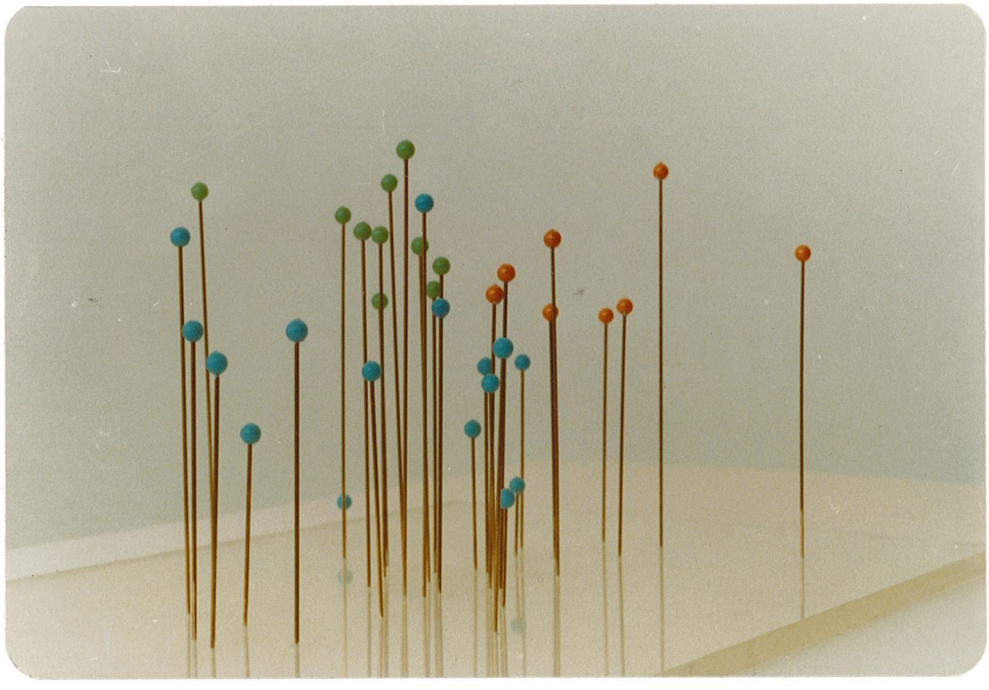


Plate 5.2

of the axis in the vertical plane. In this case the vertical plane represents the third canonical axis which accounted for the least amount of variation (16.9%).

The attempt to show the relationship between the position of groups and two environmental factors, rainfall and substrate, as shown in Plate 5.1, is probably too confusing for easy analysis. However, where the representation of environmental factors is restricted to one factor only, for example, rainfall, as given in Plate 5.2, a clearer pattern of relationship between that factor and the position of groups emerges. The relationship between larval shape (as indicated by the pattern of groups in the canonical variate analysis) and rainfall, illustrated in Plate 5.2, has been discussed more fully in the section on *rainfall* above.

Mean Water Velocities

Mean water velocities for some localities included in the canonical variate analysis are given in Table 5.22. As noted earlier, mean velocities could only be calculated where the depth, width and slope of a stream were known. Examination of Table 5.22 reveals that larvae of *S. secretus* with the narrowest, most elongate shields occur in streams with low mean velocities (at least for the greater part of each year). All other forms of *S. secretus* from the moderately wide to very wide almost circular forms occur in streams of faster mean velocities. *S. aquaticus* occurs only in streams and rivers of fairly high mean velocities.

These results agree with the correlations obtained with stream order. Ledger (1981) is the most recent of a number of researchers including Hynes (1970) and Leopold *et al.* (1964) who suggest that, contrary to popular belief among biologists, the velocity of flow in streams tends to increase rather than decrease in a downstream direction. He demonstrated that for most flow levels in the River Tweed and its tributaries,

TABLE 5.22 Mean water velocities in some localities (groups) included in the final analysis of shape differences in Tasmanian larval *Sclerocyphon*.
Stream parameters: s = slope, d = depth, w = width, R = hydraulic mean radius, $\bar{V}$ = mean velocity.

Number	Locality	s	d (m)	w (m)	R (m)	$\bar{V}$ (cm s^{-1})
1	Lambert Creek	0.001	0.1	0.3	0.049	19.8
2	Waterworks Creek	0.05	0.15	0.5	0.064	119
3	Ben Lomond Creek	0.05	0.2	0.8	0.089	144
7	Valley Creek	0.05	0.3	0.8	0.120	181
8	Township Creek	0.01	0.4	3.0	0.193	115
9	Bird River	0.015	1.0	4.0	0.447	182
10	Cataract Creek	0.01	0.4	3.0	0.193	115
11	Parsons Bay Creek	0.001	0.5	2.0	0.223	36.8
13	Browns River	0.05	0.15	0.5	0.064	119
21	Myrtle Forest Creek	0.05	0.3	0.8	0.120	186
24	Creek near Gordon Dam	0.05	0.1	0.5	0.018	51
25	Tyndall Ranges Creek	0.2	0.4	0.9	0.149	132
28	Dee River	0.001	0.2	1.0	0.09	21.6
33	Hytten Hall Creek	0.001	0.2	0.5	0.078	19.2
35	Sorell Creek	0.02	0.6	3.0	0.266	195
36	Black River	0.02	1.1	2.0	0.50	296
37	Emu River	0.015	0.7	4.0	0.33	194
38	West Swan River	0.015	1.0	4.0	0.447	182
40	Liffey River	0.01	1.0	5.0	0.467	200

in Scotland, the highest velocities occurred at the lower, flatter end of the river system. As a corollory of this it may be said that streams of high stream order are likely to experience higher velocities than those of low stream order.

5.8 Discussion

The results of this study (Section 5.7) indicate that both the use of multiple measurements to describe the shape of larval *Sclerocyphon* and the use of canonical variate analysis are appropriate methods to reveal the differences, or similarities, in larval shape exhibited by populations in Tasmanian streams and rivers. The results of the canonical variate analysis indicate that larval shape in *S. secretus*, the most common and widely spread species in Tasmania and the one studied in most detail here, varies from wide, almost circular forms to narrow tapered elongate forms, as illustrated in Figure 5.15a, b, c and d. This variation in shape appears to be continuous in nature and a west-east trend is present with the widest, almost circular forms generally occurring in the western region of Tasmania, while the narrowest, most elongate forms occur in the east.

S. aquaticus appears to be less variable in shape than *S. secretus* and usually exhibits a wide, almost circular larval shield, as illustrated in Figure 5.15c. As *S. aquaticus* occurs only in larger streams and rivers and on doleritic substrates it is possible that the lower variability in larval shape between populations is a result of a more restricted range of distribution than that of *S. secretus*. The fact that fewer groups of *S. aquaticus* (6) than *S. secretus* (34) were included in the analysis may also have influenced this result.

Figure 5.8 and Table 5.12 indicate that the groups of *S. aquaticus* resemble each other more closely than they do most groups of *S. secretus*. The exceptions to this are groups 36 and 40 of *S. aquaticus* which are

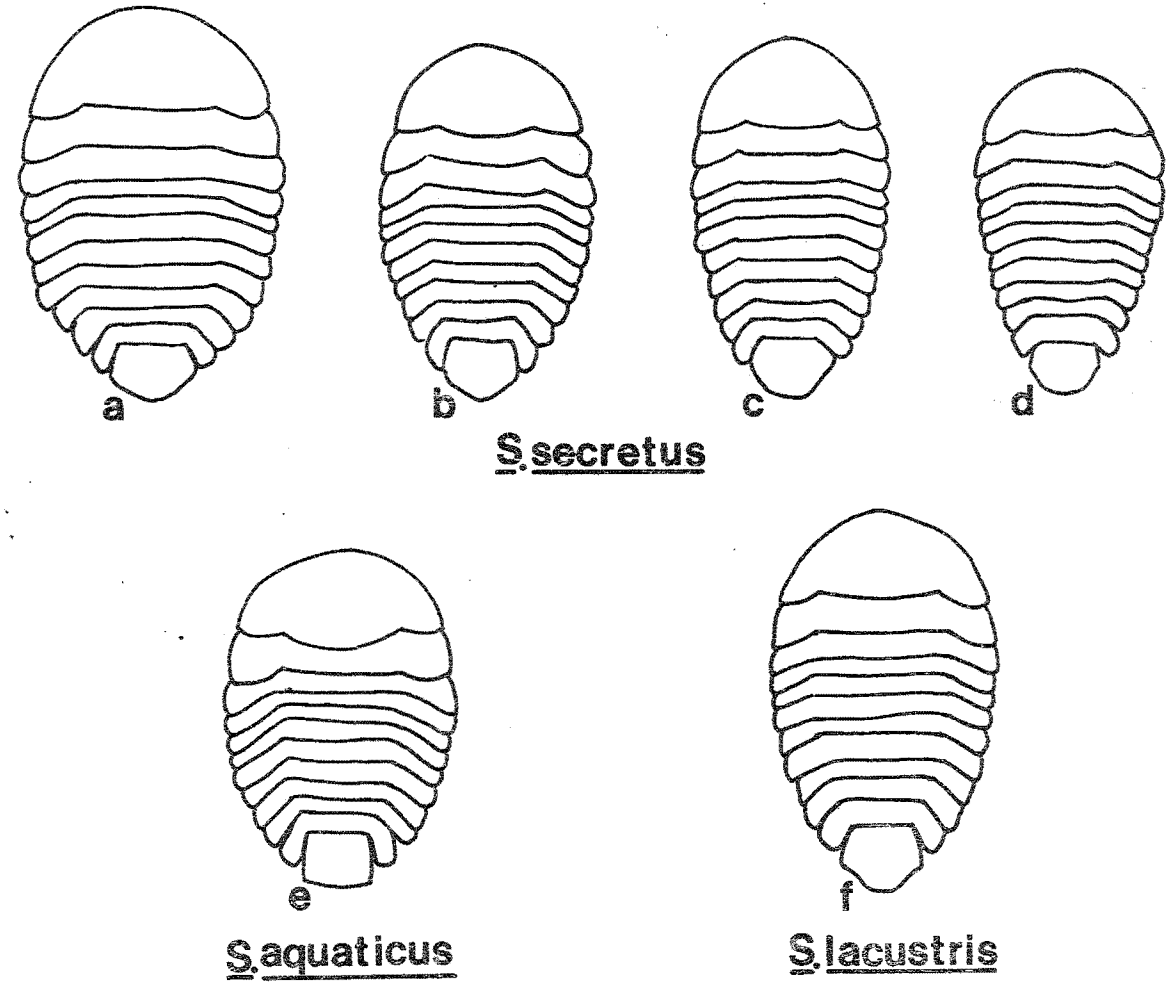


FIGURE 5.15 Larval shield shapes exhibited by *S. secretus* (a, b, c and d), *S. aquaticus* (e) and *S. lacustris* (f) as determined from the analysis of larval shape conducted on the total data set of 41 groups comprising 34 groups of *S. secretus*, six groups of *S. aquaticus* and one group of *S. lacustris*.

indistinguishable in shape from groups 8 and 4, respectively, of *S. secretus*. The reasons for this convergence of larval shape between the two species are not clear; however, this occurrence suggests that environmental factors may have some influence on the expression of larval shape.

As only one group of *S. lacustris* was included in this study, few conclusions can be made on the nature of shape variation in this species. Larvae of *S. lacustris* are usually moderately wide and tapered as illustrated in Figure 5.15f. Although the one group of *S. lacustris* (41) in the analysis does differ significantly in shape from all other groups (Table 5.12), Figure 5.8 reveals that it falls within the range of variation of *S. secretus*.

Canonical variate analysis has provided answers, in part, to both the first and second questions posed in the Introduction (Section 5.1). While the range of larval shapes that exists within *S. secretus* is well-defined, a greater number of groups of *S. aquaticus* and *S. lacustris* must be included in the analysis before the range of variation within the latter two species will be clearly known. Figure 5.15 illustrates the differences in shape evident between larvae of *S. secretus*, *S. aquaticus* and *S. lacustris* although this may have to be altered when further information on the latter two species is obtained.

It must also be noted at this point (and has already been noted in the Introduction, Section 5.1) that field observations indicate that larval shape within *S. aquaticus* and *S. lacustris* appears to be far less variable than in *S. secretus*. Therefore the emphasis upon *S. secretus* in this study was not without some justification, apart from the fact that a larger number of samples of *S. secretus* were present in the taxonomic collection.

The influence that environmental factors may have on the expression of larval shape (the third question posed in the Introduction, Section 5.1),

has also been elucidated, in part, for *S. secretus* and to a lesser extent, *S. aquaticus*, in this study. The west-east trend in larval shape of *S. secretus* has already been noted above; however, as several environmental factors (rainfall, rainfall variability, temperature and substrate) co-vary along the same west-east gradient, it is difficult to isolate the effects of a single factor.

The shape of larvae of *S. secretus* has been related to stream order, rainfall and rainfall variability, substrate, altitude and stream velocity (Section 5.7). The widest larvae of *S. secretus* generally occur in streams of high order (larger streams and rivers) in regions of high and consistent rainfall, at higher altitudes, on quartzitic substrates and in faster flowing streams. The narrowest forms usually occur in streams of low order (small streams), in regions of lower and more variable rainfall, on dolerite substrates and in slower flowing streams.

The three groups that are exceptions to these statements (the three outliers in Figure 5.10); the Meredith River (29) on the east coast (with wide larvae), the tributary of the Little Donaldson River (6) in the north-west (with narrow larvae) and Lake Pedder (30) in the south-west (with narrow larvae) all need further study as it is these exceptions to the rule that may provide the most information on the effects of environmental factors on the expression of larval shape.

As already noted it is not factors such as stream order, rainfall, rainfall variability and altitude that influence the expression of larval shape directly but rather these reflect the effect of factors of more immediate concern to larvae; in particular, water velocities and temperatures. The possible effects of temperature on the expression of larval shape will not be discussed here as this factor was not investigated sufficiently in this study. However, some comments on the effect of water velocities on the expression of larval shape can be made.

The occurrence of the narrowest, most elongate larval forms of

S. secretus in the slowest mean velocities does, in fact, represent something of a paradox as these larvae appear to be the form most suited to life in high velocity flows. Drag forces upon a submerged object depend, in part, upon the maximum cross-sectional area of the object across the direction of flow. As larvae never exceed 2.2 mm in height (Chapter 6) the narrow elongate forms must experience lower drag forces than wide forms when larvae are orientated in the direction of flow. The latter forms must then be in greater danger than the former of being swept off the substrate in high energy flows.

Similar paradoxes have been observed in other aquatic benthic invertebrates. Starmühlner (1953) found that the common European limpet, *Ancylus fluviatilis*, was taller in faster water than in slow although the snail, *Limnaea pereger*, was smaller and thicker in faster flow. Goodrich (1937 cited by Hynes, 1970) found that species of the prosobranch gastropod, *Pleurocerca*, in Alabama streams, became wider in relation to length in downstream sites.

Three alternative explanations for this apparent paradox concerning the shape of larvae of *S. secretus* can be proposed. Firstly, it is possible that no paradox exists, the larval shapes described here may represent the most efficient forms for the various flow regimes. Differences in the separation characteristics (that is, the point at which separation of the boundary layer over the larva occurs) of the different shapes were not detected by the techniques used to investigate the hydrodynamics of larvae in this study (Chapter 6); however, this does not mean that differences do not exist. It is possible that wider larvae, by possessing longer slots between the lateral laminae, may have a more efficient structure for control of their boundary layer by suction (Chapter 6) and therefore experience lower drag forces.

A second explanation may be that the shapes of larvae are determined by factors other than the direct physical effect of current. Stream-

lining and the associated mechanisms of boundary layer control (described in Chapter 6) may ensure that all larvae live in a low drag situation and further adaptations in the form of different shapes are not necessary.

The wide, almost circular, larval shield may represent the form achieved under optimal conditions for growth in an organism for which expansion in the vertical plane is restricted. Maximum accumulation of body tissue in the larval stage is advantageous as it enhances adult fecundity. However, for larval *Sclerocyphon* an increase in height (presumably beyond 2.2 mm) may well expose them to high energy flow beyond the boundary layer region of the stream bed and thus increase the risk of dislodgement from the substrate. Thus an increase in width, relative to total length, may well represent the most efficient means of increasing larval size overall. Narrow, elongate forms may therefore be a result of less than optimal conditions for growth.

Larval growth may be influenced by stream temperatures, oxygen availability and abundance and type of food supply. Table 5.23 indicates that the time taken by larvae of *S. secretus* to utilise the dissolved oxygen in a volume of water equal to their body volume is very long; 67.8, 116 and 512 hours at 25°C, 15°C and 5°C, respectively. This suggests that *S. secretus* and possibly all *Sclerocyphon* larvae are not dependent upon stream flow for their oxygen supply. The fact that larvae exhibit an active rather than passive mode of gill ventilation also suggests an independence of stream flow for respiration. Larvae can be kept alive in still waters at room temperature for several days and in aerated but still water for a year or more. These results suggest that larval growth is probably not influenced by increased oxygen availability due to either increased water velocities, decreased water temperatures or a combination of both. As a consequence it is unlikely that larval shape would be influenced by these factors if the argument, above,

TABLE 5.23 Time taken by larvae of *S. secretus* to utilise the dissolved oxygen in a volume of water equal to their body volume, at 100% saturation, at three different temperatures. Rates of oxygen consumption of larvae of *S. secretus*, at three different temperatures, are taken from a previous study on Tasmanian *Sclerocyphon* by Davis (1975).

Calculations

At $5^{\circ}C$

100% saturation of dissolved oxygen = $12.80\ mgL^{-1}$

$\therefore$ oxygen concentration = $12.8\ L\ m^{-3}$

Rate of oxygen uptake by larva (ΔDO_2) = $1.6 \times 10^{-6}\ L\ hr^{-1}$

Volume of larva (V_L) = $6.4 \times 10^{-5}\ m^3$

Time taken by a larva to use the oxygen in a volume equivalent to its body volume at $5^{\circ}C$

$$T = \frac{\text{volume of dissolved oxygen}}{\text{uptake rate}}$$

$$= \frac{\text{oxygen concentration} \times \text{volume of larva}}{\text{uptake rate}}$$

$$= \frac{12.8 \times 6.4 \times 10^{-5}}{1.6 \times 10^{-6}}$$

$$= 512$$

$\therefore$ At $5^{\circ}C$ a larva of *S. secretus* takes 512 hours to use the oxygen present in a volume of water equivalent to its body volume.

At $15^{\circ}C$

100% saturation of dissolved oxygen = $10.15\ mgL^{-1}$

$\therefore$ oxygen concentration = $10.15\ L\ m^{-3}$

Rate of oxygen uptake by larva (ΔDO_2) = $5.6 \times 10^{-6}\ L\ hr^{-1}$

Volume of larva (V_L) = $6.4 \times 10^{-5}\ m^3$

$$T = \frac{10.15 \times 6.4 \times 10^{-5}}{5.6 \times 10^{-6}}$$

$$= 116$$

$\therefore$ At $15^{\circ}C$ a larva of *S. secretus* takes 116 hours to use the oxygen present in a volume of water equivalent to its body volume.

TABLE 5.23 (continued)

At 25°C

100% saturation of dissolved oxygen = $8.38 \text{ mg } L^{-1}$

$\therefore$ oxygen concentration = $8.38 \text{ L } m^{-3}$

Rate of oxygen uptake by larva (ΔDO_2) = $7.9 \times 10^{-6} \text{ L } hr^{-1}$

Volume of larva (V_L) = $6.4 \times 10^{-5} \text{ m}^3$

$$T = \frac{8.38 \times 6.4 \times 10^{-5}}{7.9 \times 10^{-6}}$$

$$= 67.8$$

$\therefore$ At 25°C a larva of *S. secretus* takes 67.8 hours to use the oxygen present in a volume of water equivalent to its body volume.

suggesting that the widest larval shields are an expression of maximum growth is true.

Differences in larval shape, however, may be a result of diet. Larvae feed on the attached algal flora of the substratum and Hynes (1970) states that many workers have found attached algae to be more abundant in fast waters. Therefore the occurrence of wider larval forms in faster waters may be a result of a more plentiful food supply. An abundant food supply,however, should also be reflected in larval numbers and field observations indicate that the largest populations of larvae occur in the slower flowing streams, in particular, Lambert Creek and Hytten Hall Creek, where shapes were elongate.

A third explanation is to suggest that narrower larvae are, in fact, adapted to faster currents but at the microhabitat level rather than the habitat level, as described by mean stream velocity. Although the velocity of flow at any point in a stream is inversely proportional to the logarithm of the depth,the nature of the velocity gradient in the vicinity of the substrate depends upon the roughness of the bed (Hynes, 1970). Both the height of rocks and the longitudinal spacing between them influence flow near the substrate. Smith (1975) describes and illustrates (Figure 5.16) the three different types of flow occurring over rough surfaces as a result of different longitudinal spacing first recognised by Morris (1955). Possibly larvae living in deep streams or rivers of fast mean velocities but with flow near the substrate approximating any one of the three types illustrated in Figure 5.16 are able to fulfil all their food requirements by grazing within "sheltered regions". If they never have to move out into the high energy flows over the upper surfaces and leading edges, wide larval shields would not be a disadvantage; hydrodynamically, and they would be advantageous as noted earlier in that they represent an increase in size without an increase in height.

In shallow streams or rivers flowing over rocky beds (such as Lambert and Hytten Hall Creeks), rocks may act as irregularly shaped weirs, rather

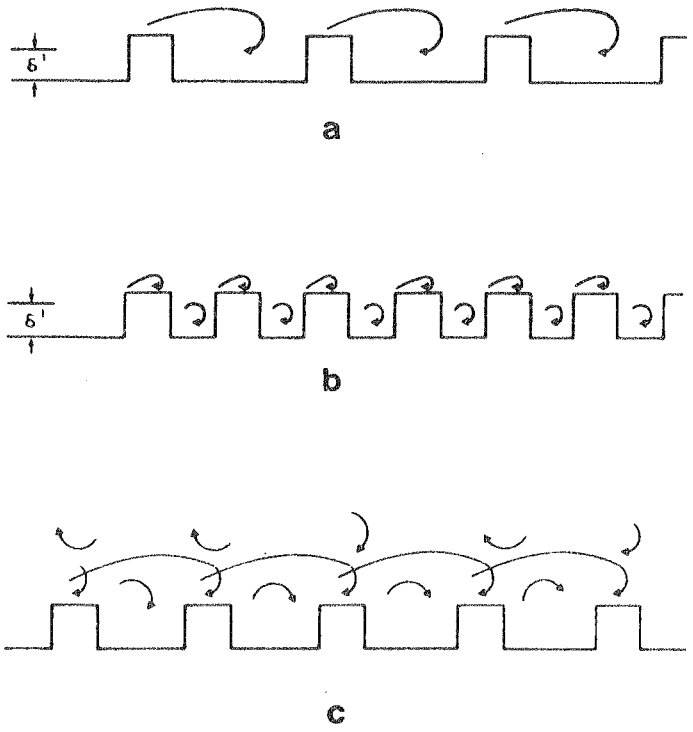


FIGURE 5.16 Morris's (1955) classification of roughness types; (a) isolated roughness (intermediate energy loss) (b) quasi-smooth flow (low energy loss) and (c) wake interference flow (high energy loss). After Smith (1975).

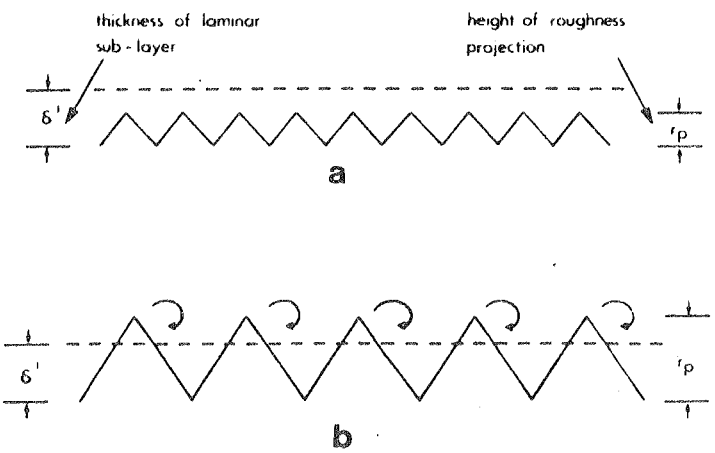


FIGURE 5.17 Two types of surface roughness; (a) smooth turbulent and (b) rough turbulent. Type (a) may represent the flow situation over quartzite in streams in western Tasmania and type (b) may represent the flow situation over dolerite in streams in south eastern Tasmania. After Smith (1975).

than roughness projections (Smith, 1975), resulting in local regions of high velocity close to the substrate. Larvae living in such streams may be forced to move across these high velocity regions to obtain food and a narrow elongate shield of minimum drag may be necessary for survival.

The occurrence of very narrow forms of *S. secretus* on doleritic substrates and very wide forms on quartzite may be explained in terms of actual surface roughness rather than bed roughness. Dolerite undergoes both physical and chemical weathering and is far rougher than quartzite which undergoes physical weathering only. Possibly the hard polished surfaces of quartzite result in smooth turbulent flow near the substrate while rough turbulent flow exists over dolerite, as illustrated in Figure 5.17, after Smith (1975). As a consequence larvae on quartzite are more likely to remain always within the shelter of the viscous sub-layer than larvae on dolerite and therefore narrow shields are more vital to the latter than the former.

5.9 Further Studies

Murvosh (1971), in an autecological study of the North American water penny, *Psephenus herricki*, found that dispersion of larvae from one particular habitat or stream to another was extremely rare. Field observations indicate that larvae of *Sclerocyphon*, similarly, remain within a fairly small region of a stream or river throughout their life. Therefore, it is conditions within the habitat, at the level of the microhabitat, that are likely to have the most influence on larval shape.

An investigation of flow conditions in the microhabitat of larvae is sorely needed. Direct velocity measurements in the region adjacent to the substrate have previously been difficult to obtain; however, recent developments in microflowmeters based on thermistor beads, and the advent of laser velocimeters, should soon make such measurements more feasible. Determinations of bed roughness and surface roughness are

also needed.

An accurate survey of the exact regions on stones occupied by larvae both within different habitats of the same stream and in different streams must also be conducted. Such a study is discussed further in Chapter 6, Section 6.7.

Since this study (Chapter 5) has found evidence to indicate that environmental factors may influence the expression of larval shape, experimental work involving the rearing of larvae in the laboratory under different,controlled conditions, or within cages in streams different to that of their origin, is now needed to isolate the effects of gene action and the environment.

CHAPTER SIX

THE HYDRODYNAMICS OF PSEPHENID LARVAE

6.1 Introduction

Even a cursory examination of psephenid larvae reveals that they possess a number of highly specialised structural features which, as noted by several authors (Hynes, 1970; Bayley and Williams, 1974), appear to be adaptations to life in the lotic environment. However, despite the distinctive form of psephenid larvae no study of their functional morphology appears to have been made.

The aim of this study was to apply the principles and practices of fluid mechanics (in particular, flow visualisation techniques) to an investigation of both the flow conditions around larvae and their adaptations to these conditions. The morphology of the larvae of *Sclerocyphon* has been elucidated, in detail, in the taxonomic study (Chapter 3), it now remains to determine the function of some of the structures described. As well, it is hoped to determine whether variation in the shape of the larval shield (as described in Chapter 5) confers any hydrodynamic advantages.

Although much is now known about the hydrodynamics of free-swimming invertebrates, in particular, fish and marine mammals, considerably less is known about invertebrates, particularly benthic invertebrates. Wu *et al.* (1977) discuss both aquatic animal locomotion and flight and Lighthill (1975) gives a detailed mathematical treatment of these topics. Both works, however, are predominantly concerned with vertebrates. Webb (1974) gives a comprehensive review of research on the hydrodynamics of fish propulsion and Aleyev (1977) has examined the adaptations of a wide range of free-swimming animals, including fish, reptiles, birds and mammals, which he collectively terms "nekton".

Nachtigall (1960) and Nachtigall and Bilo (1965) describe the hydrodynamics of free-swimming aquatic invertebrates, in particular, those of the water beetles *Acilius* and *Dytiscus*. The hydrodynamics of free-swimming micro-organisms have been investigated by a number of researchers including Taylor (1951), Hancock (1953), Gray and Hancock (1955), Brokaw (1970), Keller and Rubinow (1976), Garcia DeLaTorre and Bloomfield (1977) and Dresdner *et al*. (1980).

Studies of the hydrodynamics of benthic invertebrates, however, involves a completely different set of problems to those encountered when free-swimming animals are under investigation. Benthic invertebrates are affected by flow in the region immediately adjacent to the substrate, a region known as the boundary layer. The boundary layer concept was first introduced by Prandtl (1904 cited in Webb, 1974) who suggested that flow around or over objects could be divided into two regions. The first region, the boundary layer, is that immediately adjacent to the surface where the velocity gradient is steep; increasing from the zero velocity of the surface to that of the free stream velocity. Beyond the boundary layer is a second region, known as the outer flow, where the velocity distribution is fairly uniform. Boundary layer theory is presented, in considerable detail, by Prandtl and Tietjens (1934), Schlichting (1960), Levich (1962) and Goldstein (1965).

Ambuhl (1959) describes one of the few practical studies made of the boundary layer associated with the substrates of rocky streams and discusses the implications of the conditions in this region for the invertebrates living there. Although a number of workers have described the apparent adaptations of benthic invertebrates to fast flowing waters (these are reviewed by Hynes, 1970) the application of fluid mechanics theory to the study of these invertebrates has been limited to very few studies, notably to those of Bournaud (1963) working on trichopteran larvae and Craig and Chance (1981) working on simuliid larvae.

Undoubtedly this paucity of information on the hydrodynamics of benthic invertebrates is partly due to the difficulties involved in measuring the flow around relatively small organisms living in a boundary layer region. Recent advances in instrumentation and, particularly, the advent of laser velocity meters may make future studies much more feasible.

6.2 Some Concepts and Principles of Fluid Motion

Any discussion of the hydrodynamics of psephenid larvae must be based upon a knowledge of the fundamental concepts and principles of fluid motion. The aspects of fluid mechanics theory which are relevant to this study are outlined below. More detailed discussions of the theory of fluid mechanics are provided by a number of texts including Prandtl and Tietjens (1934), Schlichting (1960) and Shapiro (1961). Smith (1975) and Webb (1974) describe the application of fluid mechanics theory to biological studies and both works were consulted extensively during this study.

Flow Patterns and Reynold's Numbers

Three different patterns of flow may occur in moving fluids: laminar, turbulent and transitional. In laminar, or viscous, flow fluid particles move downstream in regular and smooth trajectories and may be considered to be moving in parallel layers; between which there is no significant mixing. In turbulent flow an overall downstream motion has an irregular and seemingly random motion superimposed upon it and there is considerable interchange of mass and momentum between different layers of flow. Transitional flow is partly laminar and partly turbulent.

The occurrence of turbulent flow depends on the ratio of inertial forces to viscous forces and this ratio is known as the Reynold's number, R_e.

$$R_e = \frac{VL\rho}{\mu} \qquad (1)$$

where V = velocity

L = characteristic length dimension

ρ = density

μ = viscosity

the quantities ρ and μ can be written as $\frac{\rho}{\mu}$ and given the symbol γ, called kinematic viscosity. R_e is a dimensionless number if any consistent set of units is used.

Flow is usually considered to be laminar for R_e<500, transitional for values of R_e between 500 and 2000 and completely turbulent for R_e>2000 (Smith, 1975). Stream flow is almost always turbulent, (Ambuhl, 1959; Hynes, 1970; Smith, 1975), as a result of not only stream velocities but also the roughness of the stream bed.

As well as predicting flow conditions Reynold's numbers also predict required conditions for mechanically similar flow around geometrically similar objects (Webb, 1975), and are thus of great utility in modelling flows.

Boundary Layers

The boundary layer is a region of flow past a surface, or across an object, where the fluid velocity increases from zero (at the surface) to its full value, which corresponds to external frictionless flow (Schlichting, 1960). The boundary layer is, therefore, a very thin region immediately adjacent to a solid surface, where frictional forces retard the motion of the fluid. In high Reynold's number situations, the influence of viscosity is restricted to this boundary layer region.

The thickness of the boundary layer, δ, may be defined as that distance from the bed where the velocity differs by more than 1% from the external or free stream velocity (Schlichting, 1960). Another

quantity, displacement thickness δ^* is sometimes used and this indicates the distance by which the external streamlines are displaced owing to the formation of the boundary layer (Schlichting, 1960).

For laminar flow in the boundary layer on a flat plate of length, ℓ, and with free stream velocity, V,

$$\delta = 5 \frac{\nu \ell}{V} \tag{2}$$

or the relative boundary layer thickness,

$$\frac{\delta}{\ell} = \frac{5}{R_\ell} \tag{3}$$

where R_ℓ denotes the Reynolds number related to the length of the plate, ℓ (Schlichting, 1960).

However, within a boundary layer flow may be laminar, transitional or turbulent. The thickness of a turbulent boundary layer is larger than that of a laminar boundary layer owing to greater energy losses in the former. For a turbulent boundary layer the relative boundary layer thickness,

$$\frac{\delta}{\ell} = 0.3 \ (R_\ell)^{-\frac{1}{5}} \tag{4}$$

The thickness of the turbulent boundary layer is larger than that of the laminar boundary layer owing to greater energy losses in the former.

In rivers and streams the boundary layer at the surface of the substrate is usually turbulent, however, within this turbulent boundary layer there also exists a thin layer of fluid immediately adjacent to the substrate where flow is entirely laminar. This region is known as the laminar, or viscous, sublayer. The thickness of the laminar sublayer δ' is usually taken as,

$$\delta' = \frac{11.5\gamma}{V_F} \tag{5}$$

where V_F is the friction or shear velocity at the substrate.

$$V_F = \frac{\tau_o}{\rho} \qquad (6)$$

where τ_o is the shear stress on the bed and ρ is the density.

The friction velocity and hence the shear stress on the bed can be calculated directly if the way in which velocity changes with depth, i.e., the velocity profile, is known. If the velocity profile is plotted with the depth, drawn on a logarithmic scale, then the resulting graph is a straight line and the value of the friction velocity V_F can be found from the slope of the line (Smith, 1975).

For rivers and streams where the flow is due to the slope on the water surface alone, that is, due to the gradient, the friction velocity V_F can be calculated from the relation

$$V_F = gDS \qquad (7)$$

where g = acceleration due to gravity

D = total depth of water

S = slope of the water surface

The roughness of the substrate will also have an effect on the velocity profile near the substrate. Smith (1975) gives an equation relating the friction velocity, V_F, to the mean velocity, $\bar{V}$, under rough conditions

$$\frac{\bar{V}}{V_F} = 5.75 \log \left(12\frac{D}{r_p}\right) \qquad (8)$$

where D = depth

r_p = height of roughness projections.

Thus the ratio $\frac{\bar{V}}{V_F}$ is dependent only on the ratio of water depth to the size of the roughness projections. Smith (1975) suggests that the value of $\frac{D}{r_p}$ may range from less than 5 for a shallow stream flowing over a shingle bed to more than 5000 for deep flow over a fine clay sediment. Smith (1975) using an average ratio of $\frac{\bar{V}}{V_F} = 20$ and the expression given

above (5) for the thickness of the laminar sublayer, δ^1, calculated the approximate thicknesses of the sublayer for a representative range of mean velocities. These values are given in Table 6.1 (after Smith, 1975).

TABLE 6.1 The thickness of the laminar sublayer, in streams, at different mean velocities and a water temperature of 15°C, after Smith (1975) ($\gamma \approx 0.011$ mm^{2}s^{-1}).

Mean velocity, $\bar{V}$ (cm s^{-1})	Thickness of the laminar sublayer, δ^1 (mm)
1	27
5	5.4
10	2.7
50	0.54
100	0.27

Boundary Layer Separation

Decelerated fluid particles in the boundary layer do not always remain in a thin layer adhering to the surface of an object. In some cases the boundary layer thickness increases considerably in the downstream direction and the flow in the boundary layer becomes reversed. This causes the decelerated particles to be forced outwards and thus results in the boundary layer being separated from the substrate. This phenomenon is known as boundary layer separation (Schlichting, 1960). Such separation is always associated with the formation of vortices and with high energy losses in the wake of the body.

Separation is most likely to occur around "blunt" objects where the downstream surface curves sharply away from the flow. A region of strongly decelerated flow then exists behind such objects. This is often seen in streams where stones act as bluff bodies with regions of slow flow occurring on the downstream side. The occurrence of such

regions in streams was clearly illustrated by Ambuhl (1959) using an optical method of flow visualisation and measurement.

It is not only the boundarly layer associated with the stones and pebbles of the stream bed that is of interest here but also the boundary layer existing around the psephenid larva itself. If separation occurs too early within the larva's own boundary layer then the resulting reverse eddy formed may be strong enough to dislodge the larva from the substrate.

The Origin of Drag in Fluid Flow

Three types of drag forces may be encountered by a submerged object; friction drag, form or pressure drag and induced drag.

Frictional drag depends upon the friction between the flow and the surface of an object and the magnitude of frictional drag depends upon whether the boundary layer is laminar or turbulent, as frictional drag increases steeply during boundary layer transition. The magnitude of frictional drag therefore depends on both the character (roughness) and area of the body surface.

Pressure drag depends on the difference between the dynamic pressure at the front and the rear of an object. The basic cause of pressure drag is the formation of vortices in the wake and the magnitude of pressure drag is determined primarily by the shape of the object (larva).

Induced drag is significant where there is hydrodynamic lift. As lift does not occur with psephenid larva (because water does not travel under the anterior section of the dorsal shield) induced drag will not be considered here.

The magnitude of the drag forces experienced by a submerged object are expressed in the form of a dimensionless drag coefficient, C_D, (Aleyev, 1977).

$$C_D = \frac{2D_f}{A\rho V^2} \quad (9)$$

where D_f = drag force

A = maximum cross-sectional area or the wettable surface area,

ρ = density

V = speed of movement of the object, or of fluid flow past it.

The drag coefficient may also be regarded as the ratio of actual measured drag to hypothetical drag (Smith, 1975).

The drag force, D_f, as defined in the equation above (9), is the total drag due to both friction drag on the surface of the body and the pressure drag due to the disturbance of flow around the body.

$$C_D = C_{friction} + C_{pressure} \quad (10)$$

Considering the case of a flat plate at zero angle of incidence to the flow the frictional drag coefficient is related to both R_e and the boundary layer flow conditions (Blasius, 1908, referred to in Webb, 1974). For a laminar boundary layer,

$$C_{friction} = 1.33\ R_e^{-0.5} \quad (11)$$

for a turbulent boundary layer,

$$C_{friction} = 0.072\ R_e^{-0.2} \quad (12)$$

and for a transitional boundary layer

$$C_{friction} = 0.072\ R_e^{-0.2} - 1700\ R_e^{-1} \quad (13)$$

From equations (11) and (12) it can be seen that the frictional component of the drag coefficient will be lower in laminar flow than turbulent flow at high Reynolds numbers.

The pressure drag coefficient of a flat plate normal to the

incident flow is relatively independent of R_e and shape as the drag arises almost entirely from pressure forces. Then, C_T = 1.0-1.3 (Webb, 1974).

For streamlined bodies the pressure drag coefficient, $C_{pressure}$ is calculated as a fraction of the friction drag coefficient and relates the increase in drag due to form to the ratio of length to width of the object.

$$C_{pressure} = C_f\left[1+1.5\left(\frac{d}{L}\right)^{\frac{3}{2}} + 7\left(\frac{d}{L}\right)^3\right] \qquad (14)$$

where L = length of the body

d = maximum diameter of the body (Webb, 1974).

The theories and concepts of fluid mechanics described above provided the background for the investigation of the hydrodynamics of larval Psephenidae (in particular, the larval *Sclerocyphon*) and indicated the directions which such a study should take. Obviously Reynolds numbers, rather than velocities, are important for describing stream flow while the height of the laminar sublayer is an important indicator of the flow conditions in the immediate vicinity of larvae. A knowledge of the drag forces (friction drag and pressure drag) that may affect larvae is necessary before the ways in which larvae cope with such forces can be determined. The calculation of drag forces (and drag coefficients) on larvae, however, was not attempted in this study.

6.3 Materials and Methods

Flow Tank

All experimental investigations of the flow patterns occurring around larval *Sclerocyphon* were carried out in a small, recirculating flow tank. The tank, illustrated in Plate 6.1 and Figure 6.1 was of a simple design, similar to that described by Vogel and LaBarbera (1978).

The working area of the tank was a rectangular channel of clear

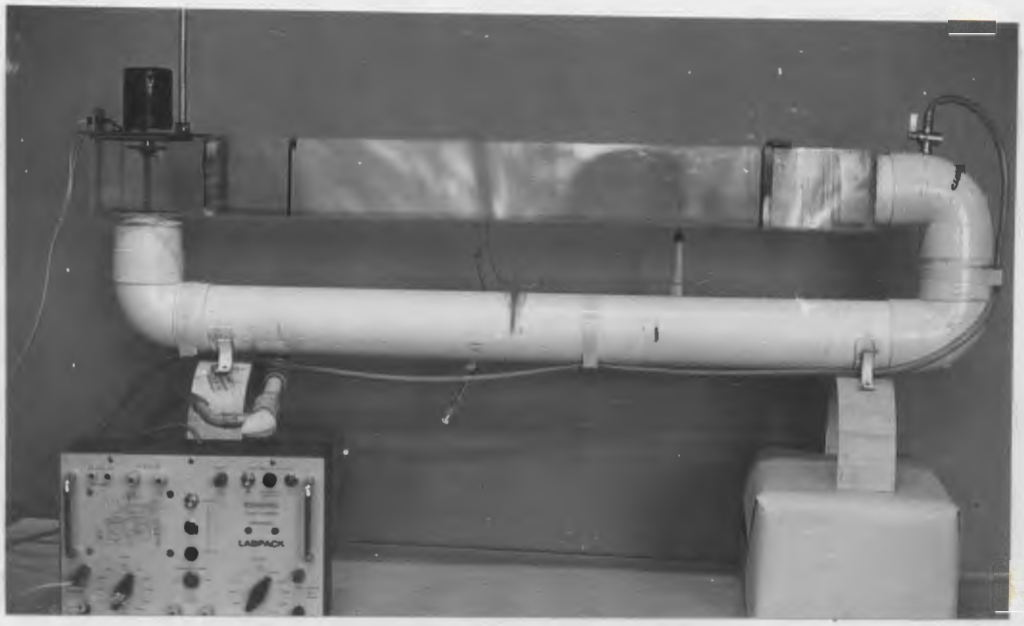


PLATE 6.1 Small recirculating flow tank used for experimental investigation of the hydrodynamics of larval *Sclerocyphon*. After Vogel and La Barbera (1978).

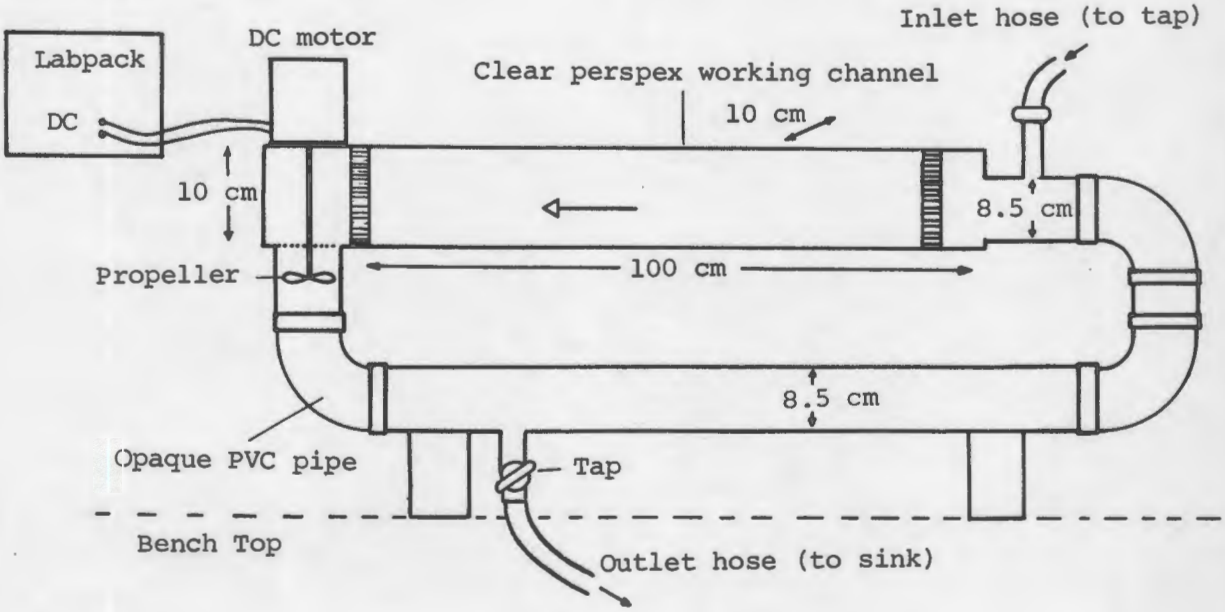


FIGURE 6.1 Diagram of the recirculating flow tank shown in Plate 6.1. A = upstream collimator of plastic drinking straws in 2 cm sections glued together. B = downstream collimator of plastic grid and flywire mesh.

perspex. Its dimensions (100 × 10 × 10 cms) were in accord with Vogel and LaBarbera's (1978) recommendation that, for smoothest flow, the depth and width of water should be similar and the length to width ratio approximately 10. The return channel was a circular pipe of PVC, 8.5 cms in diameter.

Water was circulated around the tank by a small plastic propellor, just smaller than the diameter of the return pipe (8.5 cms), powered by a small fractional horsepower DC motor connected to a variable DC power pack. A range of water velocities (0-30 cm s^{-1}) could be obtained simply by varying the output from the powerpack over a range of 0-25 volts.

The use of a rotating propellor to push water results in both axial and circular flow components, however Vogel and LaBarbera (1978) suggested that the circular component of flow could be minimized by the use of collimators. Removable upstream and downstream collimators were used. The upstream collimator consisted of an array of drinking straws fixed with silicon sealant in a removable plastic frame. The downstream collimator consisted of plastic grid, 15 mm in diameter, (normally used in fluorescent light fixtures - and often termed "egg crate") covered with plastic fly wire mesh. This also acted as a screen to catch any larvae dislodged from the substrate. At low velocities (<20 cm s^{-1}) the screen acts to reduce turbulence but at higher speeds its effect is to increase turbulence (Vogel and LaBarbera, 1978). An additional collimator of "egg crate" was placed just upstream of the propeller to further aid the propulsion of water around the tank.

Water velocities were measured, at a point just below the surface, by recording the time taken by a small plastic float weighted with a glass rod to travel 60 centimetres along the working channel. At very low velocities (5 cm s^{-1} or less) laminar conditions existed close to the substrate (Plate 6.2). At higher velocities (>20 cm s^{-1}) fully developed turbulence was present throughout the tank (Plate 6.3).

PLATE 6.2 Dye trails in flow tank with low water velocity (5 cms^{-1}) showing the presence of a laminar or viscous sublayer (1) immediately adjacent to the substrate (2). Turbulence is present above this sublayer (3). The arrow indicates the direction of flow.

PLATE 6.3 Dye trails in flow tank with higher water velocity (20 cms^{-1}). The viscous sublayer is very reduced and fully developed turbulence (1) occurs close to the substrate (2). The arrow indicates the direction of flow.

The maximum velocity recorded in the tank was 60 cm s^{-1}.

As flow phenomena around submerged objects may be extremely complex all experiments were carried out on the simplest available substrate, a flat perspex plate. As live larvae could not attach to smooth perspex a slightly roughened surface was created by glueing fine sand onto the perspex base plate. The surface of the plate, however, could still be considered hydrodynamically "smooth".

Flow patterns around larval *Sclerocyphon* were observed by placing live last instar larvae of *S. secretus* (from a number of localities), *S. aquaticus* (from Sorell Creek) and *S. lacustris* (from Lake Sorell) onto the base plate described above. Flow patterns were also observed around dead larvae, which had been glued onto glass slides and placed on the bottom of the working channel. Examination of the ventral surface of live larvae was carried out by placing larvae onto small transparent plates which had been roughened locally to permit attachment.

Flow Visualisation

A very simple method of flow visualisation was found to be the most successful. A hypodermic syringe was used to inject dye solution into the water at various points upstream of the larva. A number of different dyes including various blue and black writing inks, Indian ink, food colouring agents and milk were used. Indian ink and cochineal (a red food colouring agent) gave the clearest results.

Results of flow visualisation experiments were recorded photographically with a Petri (model FTEE) and 35 mm extension tube using black and white Ilford HP5 film at 400 ASA.

Thermistor-Based Microflowmeter

The water velocities recorded by timing a weighted float over

a set distance were surface velocities, however it was the velocities in the immediate vicinity of the larva on the bed of the tank that were of most interest here. These velocities are not easily measured. Brunditt (1971) notes that studies of the effects of current on the benthos of freshwater and tidal streams have been considerably hampered by the lack of a device capable of measuring flow near the actual animals. Such a device must be both sensitive to low velocities and possess a sensing head smaller than the organism under study. LaBarbera and Vogel (1976) designed an inexpensive hot bead thermistor flowmeter which appears to fulfil these requirements. It has a spatial resolution of 1 millimetre, a response time of 200 milliseconds and measures velocities in the range 0.2 to 50 cm s^{-1}.

A hot bead thermistor flowmeter similar to that of LaBarbera and Vogel (1976) was constructed during this study. However, it proved to be unsatisfactory mainly because adequate temperature compensation could not be achieved. A 0.5^{o}C change in water temperature resulted in a marked change in the flowmeter readings. Temperature fluctuations at this level could not be prevented and thus the flowmeter was not a satisfactory device for velocity measurement in this study. Inadequate temperature compensation appeared to be a result of the fact that thermistor beads identical to those used by LaBarbera and Vogel (1976) could not be obtained in Australia. An apparent mistake in the circuit diagram provided by LaBarbera and Vogel (1976) also prevented the exact reproduction of their design.

The failure of the thermistor-based microflowmeter to produce reliable velocity measurements meant that velocity profiles in the vicinity of a larva, and the substrate, could not be obtained experimentally in this study.

Measurement of the Vertical Force Needed to Dislodge Larvae

The force required to dislodge a larva, vertically, from the substrate was measured using a glass fibre stain gauge. The gauge was calibrated over a range of 0-5 grams and mounted on a microscope stage above the working channel of the flow tank. Fifteen centimetre lengths of cotton were glued, at one end, to the dorsal surface of live last instar larvae of *Sclerocyphon* and a small loop was left at the free end of the cotton. Larvae were removed briefly from the water and the dorsal surface dried with paper towelling before glueing.

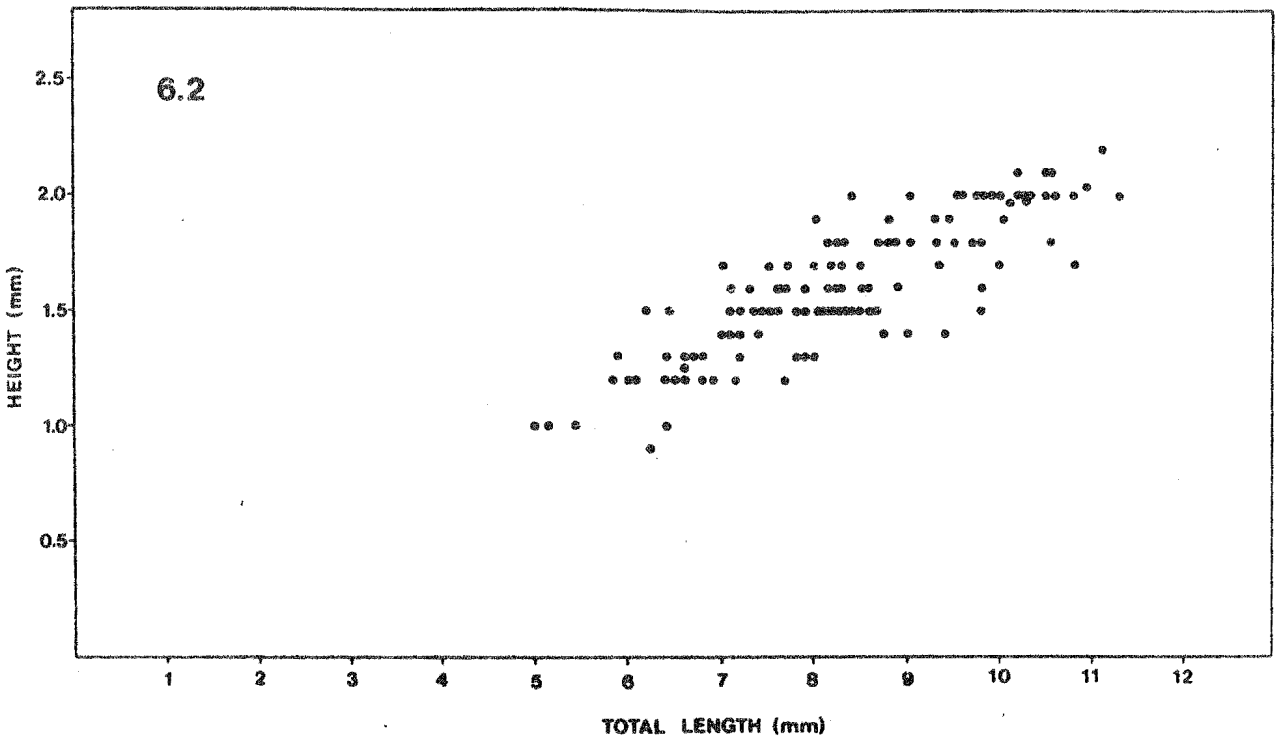
In each trial the loop of the free end of the cotton was passed over the end of the strain gauge and the whole gauge was moved slowly upwards by the means of the winding mechanism on the microscope stage. The mass required to dislodge a larva was indicated by the maximum deflection of the glass fibre strain gauge. The experiment was conducted in still water and velocities of 15, 30 and 60 cms^{-1}.

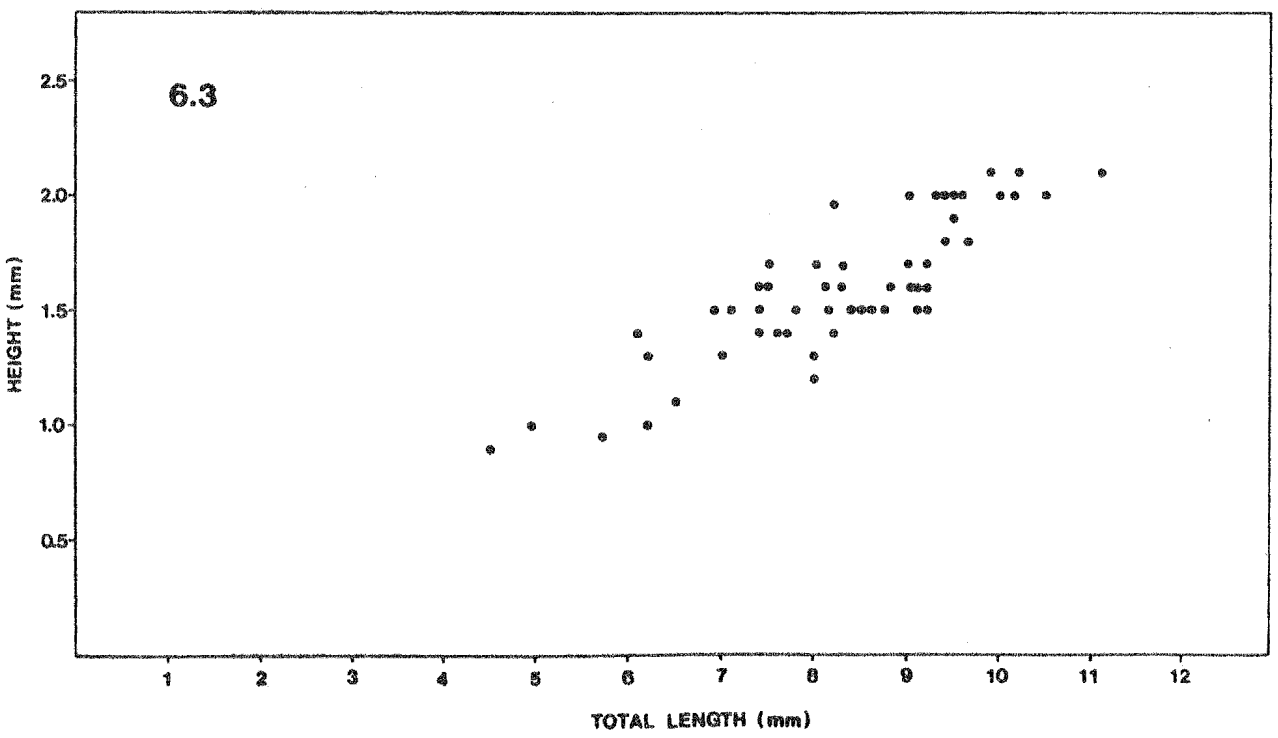
6.4 Results

Larval Height

Graphs of height against total length for 150 larvae of *S. secretus* and 75 larvae of *S. aquaticus* are given in Figures 6.2 and 6.3 respectively.

The height and length data were obtained as part of the multivariate study described in Chapter 5. Larval collection and measurement techniques are described in Section 5.2 and heights and total lengths (as well as 7 other variables) were recorded for each of 15 larvae of *S. secretus* in 10 different localities (listed in Table 5.1) and 15 larvae of *S. aquaticus* in five different localities (listed in Table 5.1).





FIGURES 6.2-6.3 Height against total length of: (6.2) larvae of *S. secretus* from ten Tasmanian localities, n = 150; (6.3) larvae of *S. aquaticus* from five Tasmanian localities, n = 75.

Initially graphs of height against total length were plotted for each locality individually. However, as few differences between localities could be detected all results were combined within each species. Where the same result was obtained for more than one larva only one point is marked on the graph.

The graphs indicate that larval height increases with an increase in total length; however, last instar larvae never exceed a maximum height of 2.2 millimetres, in either species. No further analysis of these results was necessary in this study.

Thickness of the Laminar Sublayer

The approximate thickness of the laminar sublayer in a number of Tasmanian streams, is given in Table 6.2. The thickness of the laminar sublayer, δ^1, was calculated using Smith's (1975) method where $\frac{\bar{V}}{V_f} = 20$ and $\delta' = \frac{11.5\gamma}{V_f}$ ($\gamma \doteqdot 0.011$ mm^{2}s^{-1} at 15°C) as described in Section 6.2. The mean velocities of streams listed in Table 6.2 had been calculated previously (Chapter 5, Section 5.7).

From Table 6.2 it can be seen that the thickness of the laminar sublayer ranges from 1.4 millimetres in the slowest flowing stream, Hytten Hall Creek, with a mean velocity of 19.2 cm s^{-1} to only 0.09 millimetres in the fastest flowing river, Black River, with a mean velocity of 296 cm s^{-1}.

These results must be regarded as approximations because several assumptions were made to enable their calculation. In the calculation of mean velocity, $\bar{V}$, (Chapter 5, Section 5.) a roughness coefficient of 0.03 was used for all streams whereas bed roughness was known to vary, to some extent, between different localities. Similarly where $\frac{\bar{V}}{V_f} = 20$ (above and Section 6.2) was used as a means of determining the friction velocity it was assumed that the ratio of water depth to the size of roughness projections was equal to 20 in all cases but, once

TABLE 6.2 The thickness of the laminar sublayer in some Tasmanian streams, at specified mean velocities and a water temperature of 15°C, as calculated using Smith's (1975) method (described in Section 6.2) . Mean velocities were calculated previously (Chapter 5, Section 5.7), from the data listed in Table 5.22.

Number	Locality	Mean Velocity, $\bar{V}$ (cm s^{-1})	Friction Velocity, V_f (cm s^{-1})	Thickness of the laminar sublayer, δ' (mm)
1	Lambert Ck	19.8	0.99	1.30
2	Waterworks Ck	119	5.95	0.23
3	Ben Lomond Ck	144	7.20	0.19
7	Valley Ck	181	9.05	0.15
8	Township Ck	115	5.75	0.24
9	Bird R.	182	9.10	0.15
10	Cataract Ck	115	5.75	0.20
11	Parsons Bay Ck	36.8	1.84	0.75
13	Browns R.	119	5.95	0.23
21	Myrtle Forest Ck	186	9.30	0.14
24	Ck nr Gordon Dam	51	2.55	0.50
25	Tyndall Ra. Ck	132	6.60	0.20
28	Dee R.	21.6	1.08	1.20
33	Hytten Hall Ck	19.2	0.96	1.40
35	Sorell Ck	195	9.75	0.15
36	Black R.	296	14.80	0.09
37	Emu R.	194	9.70	0.14
38	West Swan R.	182	9.10	0.15
40	Liffey R.	200	10.00	0.14

again, this would vary between different localities.

However, despite the fact that these results for the thickness of the laminar sublayer are based on assumptions, they may be still regarded as fairly realistic indicators of the laminar sublayer thicknesses that are likely to occur in streams at different mean velocities. Until an accurate means of measuring the thickness of the laminar sublayer in the field is obtained theoretical calculations of the thickness of the laminar sublayer must suffice.

Dye Visualisation of Larval Flow Patterns

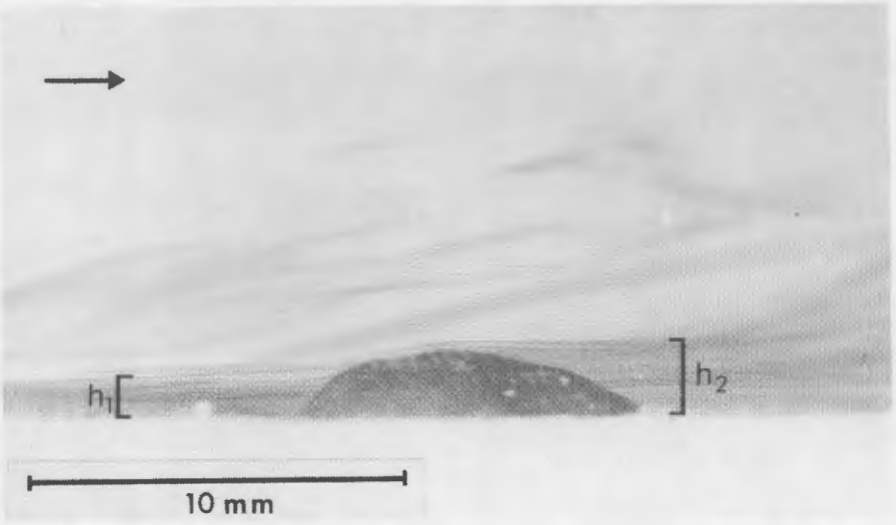
The results of the experiments in which dyes were used to trace flow patterns around larval *Sclerocyphon* are given in Plates 6.4-6.10.

Plate 6.4 is a dorsal view of a last instar larva of *S. secretus* resting on the bed of the flow tank. The photograph was taken just after Indian ink had been released at a point several centimetres upstream. Low Reynolds number conditions exist (R_e = 400, $\bar{V}$ = 5 cm s^{-1}), laminar flow predominates and the pattern of streamlines around the larva are clearly revealed by the Indian ink.

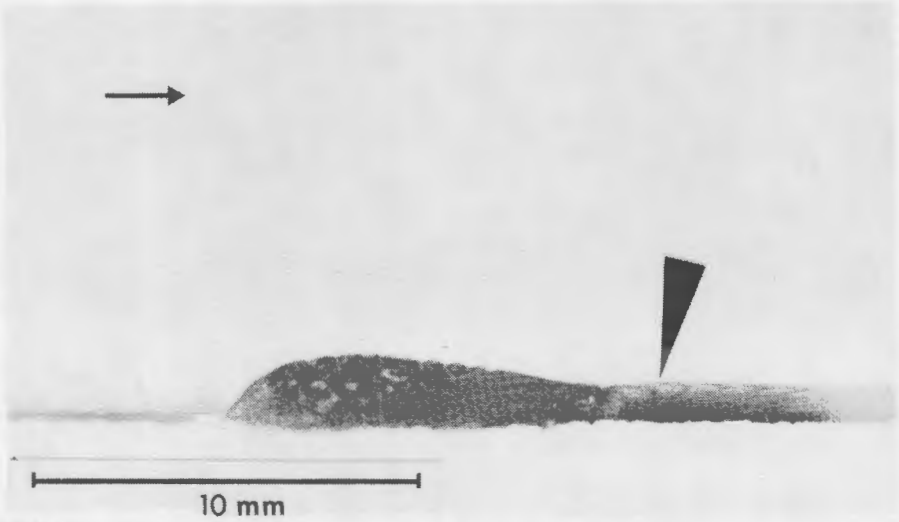
The clear region surrounding the anterior region of the larval shield is known as the stagnation zone. In this region velocities are close to zero and very little of the mainstream dye enters this zone. This region in fact represents the larva's own boundary layer. The ink trails at the rear of the larva are smooth and no turbulence is visible. Similar flow patterns were seen around both live and dead larvae of all three Tasmanian species, *S. secretus*, *S. aquaticus* and *S. lacustris*, regardless of the shape of the larval shield, when larvae were orientated in the direction of flow. Larvae positioned sideways or end-on to the direction of flow were far less streamlined with considerable turbulence evident in their wake.

Plate 6.5 is a horizontal view of a last instar larvae of

6.4



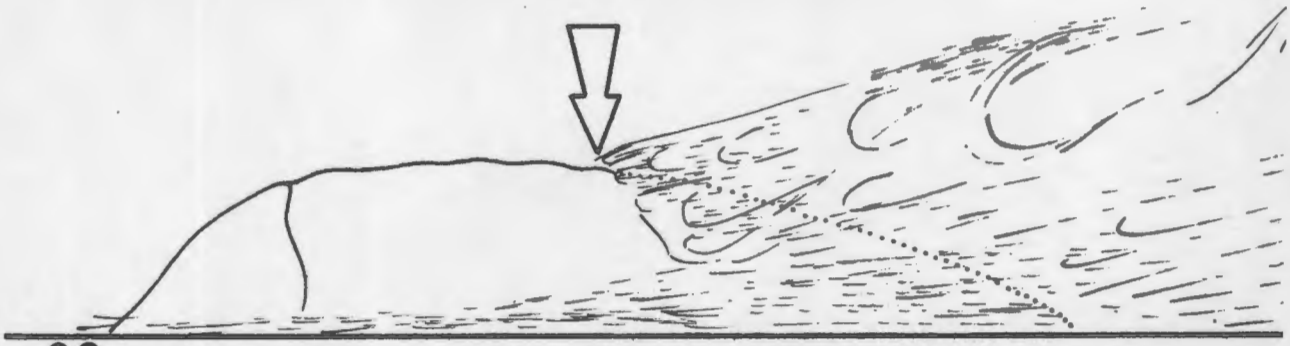
6.5



6.6

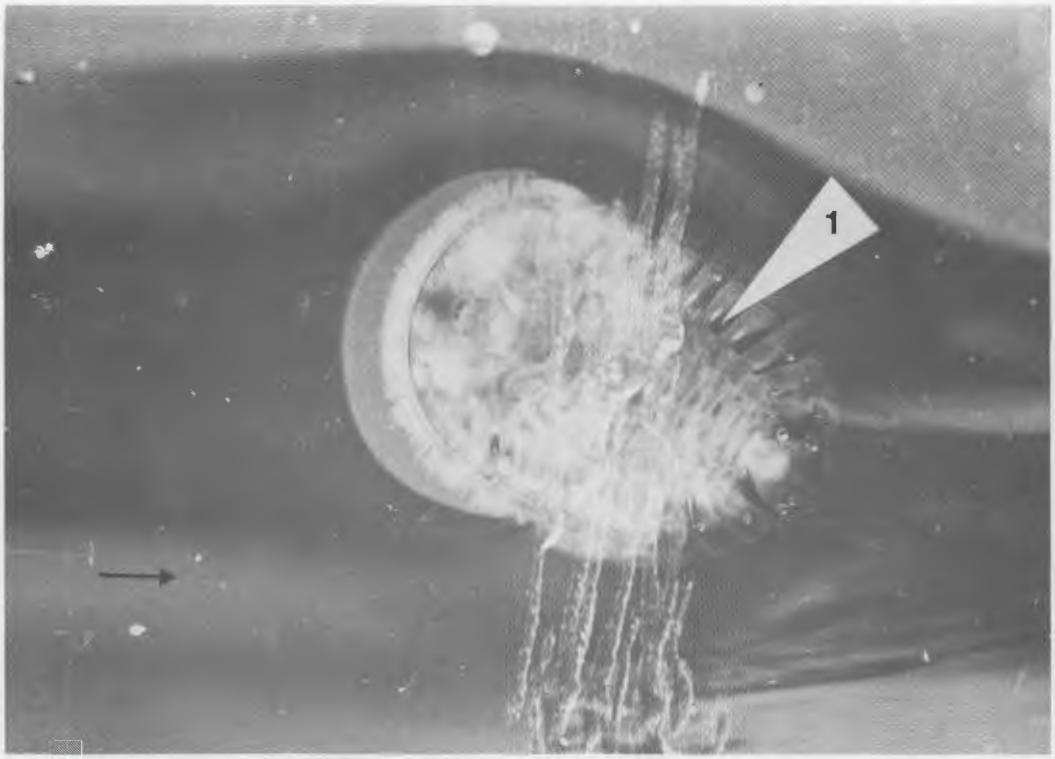
PLATES 6.4-6.6 Dye trails around larvae of *S. secretus:* (6.4) streamlines around a larva at low Reynolds number; (6.5) larva within the viscous sublayer at low Reynolds number, turbulence present above the sublayer, h_1 = height of viscous sublayer, h_2 = height of modified sublayer; (6.6) larva with anal gills actively ventilating, turbulent eddies created by ventilating gills arrowed. Flow direction (indicated by stream arrow) and scale similar for all figures.

6.7

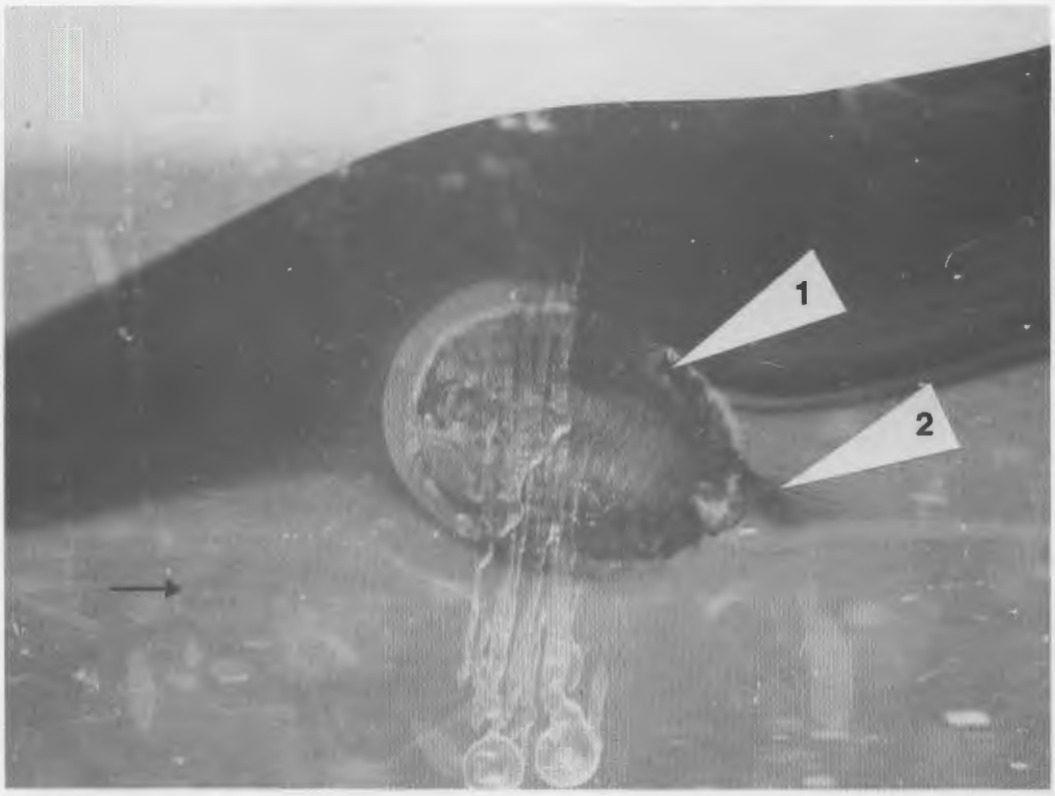


6.8

PLATES 6.7-6.8 Dye trails around larvae of *S. secretus* at high Reynolds showing boundary layer separation within the larval boundary layer (larvae approximately 10 mm long): (6.7) normal live larva; (6.8) live larva with slots between lateral laminae blocked with petrolatum. Small arrows indicate the direction of flow and large arrows indicate the point of separation in both cases.



6.9



6.10

PLATES 6.9-6.10 Ventral view of dye trails around live larvae of *S. secretus* at high Reynolds number (larvae approximately 10 mm long): (6.9) dye from boundary layer in slots (1) between lateral laminae; (6.10) dye from slots (1) moving beneath the shield and being discharged beneath the last tergite during ventilation (2). Scratches on the acrylic substrate provide attachment points for the larvae. Small arrows indicate the direction of water flow.

S. secretus resting on the bed of the flow tank. The photograph was taken just after Indian ink had been released at a point several centimetres upstream under transitional flow conditions (R_e = 1000, $\bar{V}$ = 10 cm s^{-1}). Dye trails reveal the presence of a laminar or viscous sublayer immediately adjacent to the substrate. At point h_1 the height of the sublayer is 1.2 mm. The maximum height of the larva is 1.6 mm and the height of the sublayer increases to 1.8 mm at point h_2, due to the presence of the larva. Dye trails above the laminar sublayer reveal that the remainder of the boundary layer is turbulent.

Plate 6.6 is a horizontal view of a live last instar larva taken after the main parcel of Indian ink released upstream of the larva had passed by. However, dye has accumulated in the region of slower flow at the rear of the larva. The ninth tergite is upraised, the gills which lie beneath are extruded and actively ventilating. The small turbulent eddies (arrowed) created by the actively pumping gills are clearly outlined by the dye traces.

Plate 6.7 is a horizontal view of a live last instar larva in high Reynolds flow (R_e = 3000, $\bar{V}$ = 30 cm s^{-1}) taken several seconds after Indian ink was released upstream of the larva. Separation of the larval boundary layer has occurred, the point of separation is arrowed, and flow downstream of this point is turbulent.

Plate 6.8 is a horizontal view of a larva under the same conditions as above (Plate 6.7). However, the slots between the lateral laminae on this larva have been blocked with petrolatum. Separation has occurred earlier, at a point closer to the maximum height of the larva, as indicated by the arrow.

Plate 6.9 is a ventral view of a live last instar larva of *S. secretus* clinging to a roughened transparent plate under high Reynolds number conditions (R_e = 3000, $\bar{V}$ = 30 cm s^{-1}). Dye from the boundary layer adjacent to the dorsal surface of the larva can be seen

entering the slots on the left hand side and moving through to the ventral surface. The stagnation zone is visible anteriorly as a clear region free of dye.

Plate 6.10 is a ventral view of a larva under the same conditions as above (Plate 6.9) but the ninth tergite is upraised and the larva is actively ventilating. Dye that had moved from the boundary layer into the lateral slots is now moving beneath the body shield (1) and being discharged beneath the last tergite during ventilation (2). The larvae in both Plate 6.9 and 6.10 are slightly askew rather than directly orientated in the direction of the current. In such a situation larvae adjust the slots so that dye passes through the downstream slots only.

Vertical Forces Needed to Dislodge Larvae

The forces required to dislodge last instar larvae of *S. secretus* from a flat, slightly roughened, substrate in still water and velocities of 15, 30 and 60 cm s^{-1} are given in Table 6.3. As there were only minor differences between the four different flow situations mean results were also calculated for the total data set. Although the correct unit of force is the Newton (1 kg force = 9.8 Newtons) the results of this study are expressed in grams as this latter quantity has greater biological relevance.

TABLE 6.3 Forces required to dislodge larvae, vertically, from the substrate. Mean velocity, $\bar{V}$ = mean velocity in the flow tank. Number = the number of larvae dislodged.

Mean Velocity, $\bar{V}$ (cm s^{-1})	Number	Mean Force (gms)	Range of Forces (gms)
0	25	2.45	1.0 - 4.5
15	11	2.02	1.0 - 3.2
30	20	2.74	0.8 - 4.5
60	29	2.54	1.0 - 4.5
Total Data Set			
0-60	85	2.5	0.8 - 4.5

From Table 6.3 it can be seen that the vertical force that must be applied to dislodge a last instar larva ranges from 0.8 to 4.5 grams with a mean value of 2.5 grams.

6.5 Discussion

Theoretical Predictions of Flow Conditions Around Larval Psephenidae

Individual Reynolds numbers are often calculated for free-swimming organisms as a means of predicting flow conditions in the immediate vicinity of the organism. Webb (1974) notes that a wide range of Reynolds numbers exist for individuals within the animal kingdom ranging from approximately 10^{-5} for spermatozoa to 3×10^{8} for a blue whale. For animals of low Reynolds number (<500) the dominant forces acting upon the body will be viscous while for animals of high Reynolds number (>2000) the dominant forces will be inertial. However, the exact point of transition (the critical Reynolds number) from a laminar or viscous situation to one of turbulence, and thus inertial forces, differs between species and must be determined experimentally.

Calculation of Reynolds numbers for psephenid larvae, however, does not contribute greatly to a knowledge of the flow conditions around them as they are benthic rather than free-swimming organisms. It is the flow conditions within the boundary layer of the substrate that are of utmost importance and, in particular, the thickness of the laminar sublayer. Where the thickness of the laminar sublayer is greater than the height of a larva the larva is subject to viscous forces only. As the thickness of the sublayer decreases the larva becomes increasingly exposed to turbulent flow.

Examination of Figures 6.2 and 6.3, the graphs of height against total length for larvae of *S. secretus* and *S. aquaticus* respectively, reveals that while height and length are positively related the maximum height of larvae in the last instar (the largest larvae) never exceeds 2.2 mm. This information together with the values for the thickness of the laminar sublayer, given in Table 6.1 (after Smith, 1975) indicate that all larval *Sclerocyphon* are completely sheltered by the laminar sublayer at mean velocities of 10 cm s^{-1} or less. For mean velocities greater than 10cm s^{-1} larval height may exceed the height of the laminar sublayer and thus larvae may be exposed to turbulent flow.

Examination of the values of the thickness of the laminar sublayer in some Tasmanian streams (Table 6.2) suggests that in the slower flowing streams, for example, Lambert Creek and Hytten Hall Creek, larvae of early instars are likely to remain within the laminar sublayer while last instar larvae may protrude above it and be exposed to turbulent flow. In the faster flowing streams and rivers, for example, Myrtle Forest Creek and Black River, the laminar sublayer is so reduced (0.14-0.09 mm) that larvae of most instars are likely to protrude above it. In all streams and rivers listed in Table 6.2 the thickness of the laminar sublayer is less than the maximum height attained by larvae in the last instar (2.2 mm). Some of the ways in which larvae cope with life in both laminar and turbulent flows were revealed by flow visualisation techniques and are described below.

Larval Adaptations Revealed by Flow Visualisation Techniques

Streamling

Dye visualisation of flow patterns around larvae in low Reynolds number conditions revealed that all larval *Sclerocyphon* are streamlined (Plate 6.4) when orientated in the direction of flow.

Ideally, a streamlined body has zero pressure drag in an ideal fluid. In practice, this does not occur and a streamlined body must be defined as a body that offers least resistance to fluid flow (Webb, 1974). With a streamlined body separation is delayed and occurs close to the trailing edge.

From Plate 6.4 it can be seen that the gradual posterior tapering of the larval shield directs water flow smoothly to the rear of the body. As the wake behind the larva is small the net disturbance to the flow is small and so pressure drag is also small. Drag on the larval body is therefore mainly friction drag. All larvae appear to conform with an ideally streamlined object in that their maximum width and height are achieved at about 36% along their length (Bournaud, 1963) when they are orientated in the direction of flow.

While streamlined forms are common in larger swimming organisms, they are rare among benthic invertebrates (Hynes, 1970). Baetid mayflies are the most well-known example of a streamlined benthic invertebrate although all limpet-shaped animals are also streamlined to some extent (Hynes, 1970). Craig and Chance (1981) note that simuliid larvae which are cylindrical in shape actually present a streamlined form to the current because of the manner in which they are attached to the substrate.

Modification of the Laminar Sublayer by Streamlined Larvae

Under low Reynolds number conditions when larvae are completely immersed within the laminar sublayer the streamlined shield keeps drag forces to a minimum and larvae can maintain their position on the upper surfaces of stones with minimal expenditure of energy. However, Shapiro (1961) suggests that if the drag of a streamlined object is to be kept to a minimum a laminar boundary layer must be maintained around the object at all times. Dye visualisation of flow patterns around

larvae indicates that the shape of the larval shield actually increases the height of the laminar sublayer, under certain circumstances, to ensure that the larva remains within it. This can be seen in Plate 6.5 where the height of the laminar sublayer is only 1.2 mm several millimetres upstream from a larva 1.6 mm high. The laminar sublayer in the immediate vicinity of the larva, however, increases to a height of 1.8 mm and thus a laminar boundary is maintained over the larva. This situation only occurs where the laminar sublayer is still relatively thick, at least half the height of the larva.

This result indicates that the theoretical predictions of flow conditions around larvae, based on calculations of the thickness of the laminar sublayer, given above, are not entirely accurate as the larva is capable of actively modifying the height of the sublayer in the vicinity of its body.

Respiratory Processes in the Laminar Sublayer

Maintenance of a laminar sublayer over the larval shield is of considerable adaptive advantage as drag forces are kept to a minimum enabling larvae to graze the upper surfaces of stones without risk of being washed away. However, a serious disadvantage of this situation is the fact that movement of respiratory gases within the laminar sublayer is limited to the slow rate of molecular diffusion.

Larval *Sclerocyphon* and, in fact, all larvae of the Eubriinae and Psephenoidinae overcome the constraints of this situation by creating their own respiratory current with a pair of anal tracheal gills. The retractable gills are located beneath the ninth tergite (Plate 6.11). During ventilation the tergite is lifted and the actively pumping gills are extruded. Pumping creates a turbulent area at the rear of the larval body (Plate 6.6) which does not increase drag and enhances respiratory processes and waste removal.

In high Reynolds number situations where the thickness of the laminar sublayer is so reduced that larvae are exposed to turbulence active ventilation may no longer be vital for respiration; however, under such conditions it may be a mechanism for drag reduction. The generation of small vortices at the rear of the larval body (Plate 6.6) effectively controls energy losses in the wake, keeping such losses small and so also keeping pressure drag to a minimum.

Boundary Layer Control by Suction

In situations where the laminar sublayer is so reduced that larvae must be exposed to high energy flows, it appears that they maintain position on the upper surface of stones by a further method of boundary layer control known as suction. The spaces between the lateral laminae (Plate 6.12) act as slots through which a small amount of boundary layer fluid passes. Fluid mechanic theory predicts (Schlichting, 1960; Walz, 1969), and actual suction aerofoils demonstrate (Tokaty, 1971), that suction delays separation of the boundary layer.

Schlichting (1960) states that the effect of suction is to remove decelerated fluid particles from the boundary layer before they have a chance to cause separation. A new boundary layer which is capable of overcoming a certain adverse pressure gradient then forms in the region behind the slot, as illustrated in Figure 6.4. Schlichting (1960) suggests that a suitable arrangement of suction slots will shift the point of transition, in the boundary layer, in the downstream direction. This appears to occur in larval *Sclerocyphon* where suction through the lateral laminae delays separation rather than preventing it entirely. Suction results in the larva's own boundary layer being thinner but more stable. The delay in separation reduces pressure drag and, therefore, total drag upon the larva.

Plate 6.7 illustrates the occurrence of separation towards the rear of the larval shield under high Reynolds number conditions.

6.11

6.12

PLATES 6.11-6.12 *Sclerocyphon secretus*, last instar larva from Lambert Ck, Tasmania: (6.11) ventral view, (1) operculum covering retractable gills, (2) slot between lateral laminae; (6.12) dorsal view. Larva approximately 10 mm long.

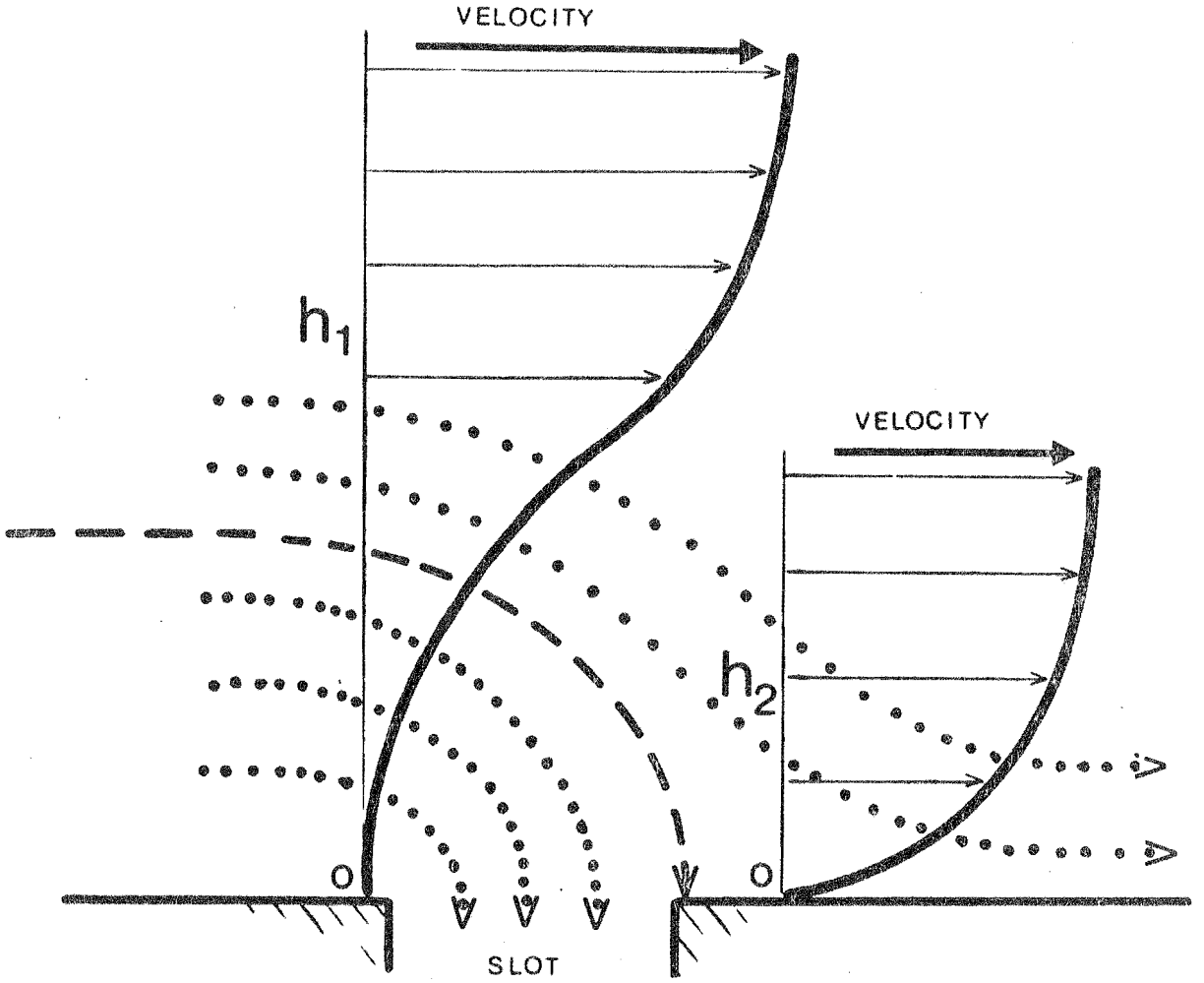


FIGURE 6.4 Theoretical velocity profiles and lines of flow in the vicinity of a suction slot. Stagnation point streamline dashed; other streamlines dotted. h_1 = initial height of velocity profile; h_2 = height of velocity profile after suction. After Walz (1969).

Similar dye visualisation of flow around a larva whose slots were blocked with petrolatum (Plate 6.8) reveals that separation occurs much earlier, soon after the point of minimum pressure, and drag forces upon the larva would be considerably higher.

When larvae were placed upon a transparent substrate, dye from the boundary layer above the larva was observed entering the slots between lateral laminae (Plate 6.9) and moving beneath the body shield to be discharged beneath the upraised ninth tergite during ventilation (Plate 6.10). Animals lying askew to the stream flow adjust slots so that dye passes through the downstream slots only.

Only a small volume of fluid needs to be removed by suction to maintain boundary layer control (Schlichting, 1960). Larvae may be able to control suction by the adjustment of the volume under the body, both by muscular activity and active ventilation.

The ability to control their boundary layer by suction ensures that larvae experience minimal drag forces even at times of rapid increase in stream flow. Such increases in shear stresses occur during stream spates and even when the animal changes position in the habitat.

Boundary layer control by suction also appears to occur in the larvae of the two subfamilies, the Psepheninae and Eubrianacinae, which possess passive ventral tracheal gills. Examination of preserved specimens and illustrations (Hynes, 1970; Blackwelder, 1930; West, 1929b) of larvae with ventral gills has revealed that suction through slots may be the only means of maintaining adequate waterflow over the gills in those animals. The ventral gills of *Psephenus herricki* are illustrated in Plate 6.13.

In *Psephenus herricki* (Plate 6.14) a thin joint of soft flexible tissue is present at the junction between each lateral lamina and the body. This enables each lamina to move in both the horizontal and vertical planes. This is not the case in *Sclerocyphon* and all other Eubriinae where the body and lateral laminae are covered with a continuous

6.13

6.14

PLATES 6.13-6.14 *Psephenus herricki*, larva from Oakville Ck, Ontario, Canada: (6.13) ventral view, (1) ventral gills; (6.14) dorsal view (1) thin flexible joint at junction of lateral lamina and body, (2) ridge on lateral lamina. Larva approximately 8 mm long.

sheet of chitin and movement of the lateral laminae is restricted to the horizontal plane only. Larvae of *Psephenus herricki* therefore appear to have greater control over both the width and orientation of slots between laminae. Such control may be very necessary when respiration depends largely on the movement of water through the slots. A ridge along the entire length of each lamina, behind each slot, may also serve to direct water movement through each slot.

Further Adaptations to Life in Running Water

Forces Used by Larvae to "Grip" the Substrate

Flow visualisation techniques could not, of course, reveal all the mechanisms employed by larvae to maintain position in the benthic habitat. Larvae also exert a powerful grip upon a rough substrate using the thoracic legs. The importance of the legs in maintaining position first became evident when larvae were unable to maintain position, even at very slow velocities (5 cm s^{-1}), on a completely smooth perspex plate. However, a slight roughening of the surface of the perspex with fine grade glass paper produced a satisfactory surface for larval attachment. It appears, therefore, that even the smallest roughness projections will provide a point of purchase for the stout tarsal claws of the larvae.

The forces needed to overcome a larva's grip on the substrate and dislodge it, vertically, range from 0.8 to 4.5 grams with a mean value of 2.5 grams (Table 6.3), for last instar larvae. The force that a larva can exert to withstand vertical dislodgement is thus considerable relative to its body mass which, for last instar larvae, ranged from 0.003 to 0.005 grams. Such a "gripping" ability would be of considerable aid in preventing dislodgement by predators such as patypus (Faragher *et al.*, 1979), trout (Jackson, 1978), freshwater flathead (Hortle and White, 1980) and freshwater turtles (M. Notestine, pers. comm.).

At first it was thought that the force required to dislodge larvae vertically may also represent the force exerted by larvae to overcome drag forces on the body; that is, the shear stresses which would tend to push the larvae downstream. However, forces required for vertical dislodgement cannot be related to drag forces which, in fact, have a major horizontal component. Therefore, while the former forces give some indication of the ability of larvae to resist predators they cannot be regarded as a measure of the magnitude of drag forces upon larvae.

The experimental assessment of drag forces upon a benthic invertebrate and the associated computation of drag coefficients is a complex procedure and was not undertaken during the present study. Bournaud (1963) obtained estimates for the forces experienced by a trichopteran larva, *Micropterna testacea*, by considering the forces acting upon cylinders of similar size. The theory of forces upon cylinders is well documented in fluid mechanics literature but while the case of a caddis larva may be validly likened to a cylinder the same analogy cannot be applied to a psephenid larva. An appropriate starting point for any future study of drag forces upon larval Psephenidae may be to liken a larva to a flat plate of equivalent wettable surface area.

Mucus

The taxonomic study (Chapter 3) revealed the presence of mucus over much of the dorsal shield of the larvae. In particular, the highest structures projecting from the shield, the mid-dorsal clumps of sensillae, were always covered with mucus.

Toms (1948) demonstrated that small quantities of high molecular weight polymers flowing in tubes produced friction drag coefficients lower than those predicted for Newtonian fluids. A similar hydrodynamic function has been postulated for mucus secreted by aquatic organisms.

Daniel (1981) notes that mucus secretion and its role in drag reduction can be seen in a variety of biological situations. A number of studies (noted by Webb (1974) and Aleyev (1977)), have shown that fish mucus reduces friction drag and Hoyt (1970) has shown that mucus from marine organisms such as algae and bacteria can reduce drag.

Probably the mucus on the dorsal shield of larval Psephenidae is playing a part in reducing friction drag on the larvae. However, this hypothesis must be tested experimentally before the role of mucus in the hydrodynamics of larval Psephenidae is truly understood.

Surface Roughness

The taxonomic study (Chapter 3) also revealed the presence of small thickly sclerotised projections or "beads" on the dorsal shield of most larval species of *Sclerocyphon*. Depending on Reynolds number and the influence of shear stresses, surface protrusions on an object or animal may trigger separation earlier than would be expected if the same object or animal was completely smooth. This results in the boundary layer over an object becoming turbulent sooner but the wake is smaller and, therefore, pressure drag on the object is lower (Shapiro, 1961). Reduction of pressure drag through surface roughness is usually a feature of bluff rather than streamlined bodies and Shapiro (1961) illustrates this phenomenon with the example of dimpled golf balls travelling further than smooth ones.

While it is tempting to speculate that the cuticular beads of larval *Sclerocyphon* act to reduce pressure drag on the larval shield, the fact that the shield is streamlined (and therefore friction drag rather than pressure drag is of primary concern) suggests that this is probably not the case. Possibly the thickly sclerotised beads are a source of mechanical strengthening or reinforcement for the larval shield. Such strengthening may be a very necessary adaptation for organisms

living in a region of high shear stresses. Such shear stresses are a predominant feature of both the benthic boundary layer and the laminar sublayer.

The role of mucus may be intimately tied to the presence of the cuticular beads. The beads provide mechanical strengthening to the dorsal surface without requiring a hard, rigid surface over the entire shield. While such a rigid surface (if smooth) may reduce friction drag it would also restrict locomotion and body movements in general. Flexibility of the larval shield is important as it enables larvae to remain closely adpressed to rock surfaces, which may be highly uneven, while grazing. This is necessary for larvae to remain, as far as possible, within the laminar sublayer. As well it also prevents water moving under the anterior end of the shield and creating a "lift" effect which would result in the larva being swept off the rock. The role of mucus, therefore, may be to counteract the roughness effect of the beads and create a smooth surface overall. In this way friction drag upon the shield is kept to a minimum without sacrificing the flexibility of the shield.

Surface roughness or sculpturing appears to be a feature of a number of aquatic benthic invertebrates. Hynes (1970 citing Hora, 1930) notes that many blepharicerid larvae living in swift water are elaborately sculptured or spiny while Craig and Chance (1981) note that simuliid larvae have small scales and hairs on their body surface. The role that surface roughness or sculpturing plays in the adaptation of benthic invertebrates to running water needs further investigation.

6.6 Conclusions

Hynes' (1970) suggestion that the flattened form of psephenid larvae enables them to live within the relatively slow-moving boundary layer region of stones on the stream bed can now be modified, slightly,

to state that larvae are predominantly occupying the region of viscous flow, within the boundary layer, known as the laminar sublayer. The streamlined larval shield and the active mode of gill ventilation are both adaptations to life within the laminar sublayer.

In high Reynolds number situations where the laminar sublayer is so reduced that larvae must be exposed to turbulence they employ a form of boundary layer control known as suction to keep drag forces to a minimum.

The results of this study suggest that larval *Sclerocyphon* and probably all larval Psephenidae have achieved, through the processes of evolution, an optimal design for life on rocky substrate in running waters. The force of water increases as the square of the velocity and Hynes (1970 citing Bournaud, 1963) suggests that the force of 0.5 gm mm^{-2} which, theoretically, exists at a velocity of 300 cm s^{-1}, would be impossible for small animals to resist. Larval *Sclerocyphon* avoid such forces by both sheltering within the slow-moving laminar sublayer and employing very efficient means of drag reduction in situations where turbulence and higher velocity flows cannot be avoided. Thus larvae can move across the upper surfaces of stones to graze attached algae without risk of dislodgement. They are, in fact, able to exploit a food resource which is unavailable to many other benthic invertebrates not possessing their hydrodynamic advantages.

6.7 Further Studies

Although the present study has revealed much about the flow conditions experienced by larval Psephenidae the actual water velocities present in the immediate vicinity of the larva still need to be determined directly.

Ambühl (1959) demonstrated the occurrence of many regions of reduced flow in the vicinity of stones on the stream bed. An ecological

or "microecological" study of the distribution of larvae within the microhabitat, that is, over individual stones, must now be carried out to determine the exact regions preferred by them. Although larvae have mechanisms to cope with both slow and fast water flow it still remains to be determined how often these various mechanisms are employed.

Larval streamlining is only effective when larvae are orientated in the direction of flow; however, control of their boundary layer by suction through slots between the lateral laminae appears to be effective when larvae areboth orientated in the direction of flow or askew to the direction of flow. Information must now be obtained on the behaviour of larvae under different flow conditions and, in particular, the orientation of larvae under different flow conditions.

Attempts to obtain such information during the present study were hampered by the fact that larval *Sclerocyphon* are extremely negatively phototropic. This means that larvae only move across the upper surfaces of stones to graze at night (or in overcast weather conditions). Studies on the behaviour of larvae under different flow conditions must be carried out in darkness (or low light conditions) if rheotropic effects are to be separated from phototropic effects. Similarly the ecological or "microecological" studies suggested above should be conducted at night, as well as during the day, if an accurate picture of the interaction between larvae and running waters is to be obtained.

The study of differences in the shape of the larval shield in Tasmanian *Sclerocyphon* (Chapter 5) indicated that the shape of the larval shield is related, at least in part, to the flow conditions in which the larva lives. One of the aims of this study (Chapter 6) was to determine whether, and how, these different shapes may confer different hydrodynamic advantages to larvae. While the use of flow visualisation techniques revealed much about some aspects of larval

hydrodynamics, differences between the different larval shields were not detected. Further studies on the hydrodynamics of larval *Sclerocyphon* (as outlined above) may therefore also provide more information on the relationship between larval shield shape and water flow.

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APPENDICES

APPENDIX A — Identification lists for Victorian *Sclerocyphon* in the collections of the Survey Department, National Museum of Victoria made as part of the following surveys: Gippsland Rivers Environmental Survey, Dartmouth Environmental Survey, and Latrobe River and Traralgon Creek Survey.

APPENDIX B — Tables of Mahalanobis distances compiled from the canonical variate analyses used to analyse differences in the shape of larval *Sclerocyphon* (as described in Chapter 5).

APPENDIX C — Supporting papers.

APPENDIX A

Identification lists for Victorian *Sclerocyphon* in the collections of the Survey Department, National Museum of Victoria made as part of the following surveys: Gippsland Rivers Environmental Survey, Dartmouth Environmental Survey, and Latrobe River and Traralgon Creek Survey.

All *Sclerocyphon* listed overleaf were collected by members of the Survey Department, National Museum of Victoria and identified by the present author.

Table A-1 Identification list for *Sclerocyphon* in samples from the Thomson River and associated rivers and streams collected from 1976-1979 as part of the Gippsland Rivers Environmental Survey

Site	Locality	No.	Date	Species						
				Adults			Larvae			
				S. striatus Lea	*S. maculatus* Blackburn	*S. basicollis* Lea	*S. striatus* Lea	*S. maculatus* Blackburn	*S. basicollis* Lea	*S. zwicki* sp.n.
TI	Thomson R. Thomson Valley Rd.	I	11/2/77							1e
T2	Thomson R. Thomson-Portal Rd.	I	10/2/77				IL	1e		
		3	10/2/77		I					
		3	10/2/79					2e 1L		
		4	2/5/77					1L		
		I-V	25/11/76					3e		1e
T3	Matlock Creek. Mt Gregory Track	I	10/2/77					4e		
		2	10/2/77					1e		
		3	10/2/77					1e		
		4	10/2/77					3e 2L		
		4	10/2/77					3e 2L		
		I-5	25/11/76					1e		
T4	Matlock Creek,off Thomson Portal Rd.	I	10/2/77					1e		
		I	2/5/77					1e		
		I	24/11/76					1e		
		3	10/2/77					2e		
		18	25/10/77					1e		
T5	Thomson R., Thomson Portal.	I	25/11/76					3e		
		4	9/2/77				1e	2e		
T6	Thomson R.,Thomson-Jordan Divide Rd.	I	1/5/77				1L	1e		
		I	1/3/78					1L		
	sorted substrate	I	1/3/78				2e		2e	
	bulk substrate	2	1/3/78				3e			
		2	13/8/77					1L		
		2	25/11/76				2e			
	bulk substrate	3	1/3/78						1e	
		4	12/2/77				1e			

Table A-1 (cont'd)

Site	Locality	No.	Date	Species: Adults: S. striatus Lea	Adults: S. maculatus Blackburn	Adults: S. basicollis Lea	Larvae: S. striatus Lea	Larvae: S. maculatus Blackburn	Larvae: S. basicollis Lea	Larvae: S. zwicki sp.n.
T6	cont'd Bulk substrate	4	1/3/78					2e		
		5	1/3/78					1e		
T7	Thomson R., 1/2 km d.s. of Eastern Portal.	2	12/2/77				1e			
T9	Whitelaw ck. at Whitelaw Portal	3	11/2/77					2e		
		2	11/2/77					1e		
		5	2/5/77				3e			
T10	Thomson R.-BBck. jn Jericho	1-4	28/11/76					4e 1L		
		2-5							1e	
		3-5	28/11/76					1e		
T11	Thomson-Jordan jn Swingler Portal.	I	1/5/77				1e			
		A	24/11/76				1e			
		A1	24/11/76				4e			
		3	12/2/77				3e			
		3	1/5/77						1L	
		5	12/2/77				1L			
		5	24/11/76					1e		
		9	12/2/77				1e	1e		
		10	12/2/77				1e			
		10	1/5/77				1L			
		4	1/5/77				1L		1L	
		-	12/11/77				1e 1L			
T12	Thomson R. Aberfeldy Rd. 1/2 km downstream of Swingler.	I	13/2/77				2e			
		I	1/5/77				1L	1L		
		3					2L			
T13	Thomson R. Bells Clearing	I	10/2/77				1L 2e			
		I	13/8/77						1L	
	sorted substrate.	I	28/2/78						3e	

Table A-1 (cont'd)

Site	Locality	No.	Date	Species: Adults: S. striatus Lea	Adults: S. maculatus Blackburn	Adults: S. basicollis Lea	Larvae: S. striatus Lea	Larvae: S. maculatus Blackburn	Larvae: S. basicollis Lea	Larvae: S. zwicki sp.n.
T13	Thomson R. Bells clearing, contd.	3	27/2/78				1e			1e
	Sorted substrate	4	27/2/78				2e 1L			
	Sorted substrate	5	27/2/78				3e			1e
		-	9/2/77	1♀						
			25/2/78	1♂ 1♀						
T14	Thomson R. 12 km NNW of Walhalla	I(v)	26/11/76				1e			
T15	Thomson R.	IA	24/10/77				1e			
		I	2/3/78							1e
		I	2/3/78				5e			
	Sorted substrate	4	2/3/78				1L			
	Sorted substrate	5	3/3/78				2L			
T16	Thomson R. 6.9 km NW of Walhalla	I	3/5/77				1e			
		IA	22/10/77				1e			
		I	26/11/76				1e			
	Sorted substrate	I	2/3/78				2e			
		-	2/3/78				1e 1L			1e
	Sorted substrate	2	2/3/78				2e			1e
	Bulk substrate	2	13/2/78				1e			
		2	2/3/78				1e			
	Bulk substrate	3	2/3/78				3e			
		3	2/3/78							
		4	13/2/77				2e			2e
	Bulk substrate	5	3/3/78				5e			
	Sorted substrate	5	2/3/78				2e			
T18	Aberfeldy R. Donellys Ck Track	1-4	29/11/76				2e			
		-	29/11/76				4e			
		2-5	29/11/76				1e			

Table A-1 (cont'd)

Site	Locality	No.	Date	Species: Adults: S. striatus Lea	Adults: S. maculatus Blackburn	Adults: S. basicollis Lea	Larvae: S. striatus Lea	Larvae: S. maculatus Blackburn	Larvae: S. basicollis Lea	Larvae: S. zwicki sp.n.
T18	Aberfeldy R. Donellys ck Track	2-5	29/11/76							2e
	cont'd.	3	13/2/77						1e	
		3-5	29/11/76				1e			
T19	Aberfeldy R. Aberfedly-Walhalla Rd. Bridge.	I	16/8/77				1e			
		I	4/5/77				1L			
		2-5	27/11/76				4e 3L			
		2-4	27/11/76				1e			
		2	4/5/77				1e			
T20	Thomson-Aberfeldy Jn Fingerbox	2	4/5/77				3e 1L			1e
	Spur Track	4	4/5/77				1L			
T21	Thomson R. Moe-Walhalla Rd.	IC	24/10/77					1L		
		2	4/5/77				1e			
		3-5	27/11/76				2e 1L			
		4	13/2/77				23e 1L			
		4	16/8/77				1L			
		4-5	27/11/76				1e			
T21A	Thomson R. Bruntons Bridge	3	5/5/77				1e 1L			
T23	Rainbow Ck. Cowarr-Seaton Rd.	3	18/2/77				15e			
T25	Thomson R. Tinamba-Rosedale Rd.	I	19/2/77				1e			
T22	Thomson R. 4 km U/S of Cowarr Weir	4	4/10/76 7/5/77				1e 1L			

Table A-1 (cont'd)

Site	Locality	No.	Date	Species: Adults: S. striatus Lea	Species: Adults: S. maculatus Blackburn	Species: Adults: S. basicollis Lea	Species: Larvae: S. striatus Lea	Species: Larvae: S. maculatus Blackburn	Species: Larvae: S. basicollis Lea	Species: Larvae: S. zwicki sp.n.
MC I	Upper Macalister R. above Howitt Plain.	3	15/11/77							
		3	22/2/77							
	Light trap - dried specimen. 1*	-	22/2/78							
MC 6	Caledonia R. Below jn of branches. I		22/2/78							1e
		2-5	30/11/76							4e
		4								1L
MC 7	Dingo Ck Caledonia R. track.	3-5	30/11/76				1e			1e
		5-5	30/11/76							1e
		6-5	30/11/76							1e
MC 9	Shaws Ck Bennison plains	I	15/11/77						1e	
MC 10	Macalister-Caledonia R. jn	I	6/5/77				2e 2L			2e 1L
		IA	24/2/78				1e			
		IB	24/2/78							2e
		1-5	1/12/76				1e			1e
		2-5	1/12/76				2L			
		2-5	1/12/76				3e 1L			1e
		2-u	1/12/76				17e 1L			
		2-5	1/12/76				1e			1e
		3-U	1/12/76				1e			
		3	6/5/77							1L
		4	6/5/77							1e
		4A	24/2/78				3e			
		4B	24/2/78				8e			25e
		4C	24/2/78				5e			1e
		5	6/5/77				1e			
	Dried specimen	4	6/12/77			1♂				
	Dried specimens 1*	-	16/2/77	3♀♀ 1♂						

* both S. zwicki sp.n.

Table A-1 (cont'd)

Site	Locality	No.	Date	Species: Adults: S. striatus Lea	Species: Adults: S. maculatus Blackburn	Species: Adults: S. basicollis Lea	Species: Larvae: S. striatus Lea	Species: Larvae: S. maculatus Blackburn	Species: Larvae: S. basicollis Lea	Species: Larvae: S. zwicki sp.n.
MC 10	Macalister-Caledonia R.	-	16/2/77							
	dried specimens	-	16/2/77	10♀♀ 10♂♂						
MC 14	Barkly Macalister Jn Lyndon Flat	IB	24/2/78				1e			
		IA	24/2/78				1e			2e 3L
		2	12/8/77							1e
		-	17/8/77							1L
		3	6/12/77				8e			
		3B	24/2/78				1e			
		3C	24/2/78				18e			1e
		4	5/5/77				2e			2e
		4B	24/2/78				2e			
		4C	24/2/78				1e			
		5	17/8/77				1e			
		6	5/5/77							1e
MC 18	Dolobrook R. Brandy Pinchmine	1-5	2/12/76				4e 2L			
		-	2/12/76				4e 2L			
MC 19	Wellington R. 23.5 km N.N.E. of Licola on Tamboritha Rd.	I	24/2/78				2e			
		3A	25/2/78							
		3B	25/2/78				1e			
		4	24/2/78							1L
	dried specimens	-	14/11/77	3♀♀ 16♂♂						
MC 20	Macalister-Wellington R. jncs.	1A	23/2/78							1L
		I	6/5/77				1L			
		I-U	1/12/76				1e			
		2-U	1/12/76				1e			
		2-5	1/12/76				1e			
		2	6/5/77				5L			
		3	6/5/77							

Table A-1 (cont'd)

Site	Locality	No.	Date	Species: Adults: S. striatus Lea	Species: Adults: S. maculatus Blackburn	Species: Adults: S. basicollis Lea	Species: Larvae: S. striatus Lea	Species: Larvae: S. maculatus Blackburn	Species: Larvae: S. basicollis Lea	Species: Larvae: S. zwicki sp.n.
MC 20	Macalister-Wellington R. Jn	3	6/5/77				1e			
		4	6/5/77							1L
		4	23/2/78				3e			1e
		8	6/5/77				2e			
	dried specimens	-	23/2/78	1♀ 1♂						
MC 21	Macalister R. 7.3 km N.N.W. of Glenmaggie weir.	I	23/2/78				4e			
		I	17/8/77				1e			
		4	23/2/78				1e			
MC 22	Macalister R. 0.5 km below Glenmaggie weir	I	23/2/78				5e			
		3	18/8/77				1e			
		3	4/12/76				3e 2L			
MC ?	Macalister R. 6 km N.N.W. of Glenmaggie. Dried specimen A.A. Calder.	-	4/12/76	1F						
MC23	Macalister R. Manson Bridge. Newry-Tinamba Rd	I	4/12/76				2e 5L			
MC ?	Macalister R. 9 km N.N.E. of Heyfield		4/12/76			2♂♂ 1♀				
?	Wellington-Carey R. Jn - dried specimens A.A. Calder.		15/2/77	8♀♀ 6♂♂						
S4	Hellfire Ck		22/2/78				2e			

Table A-2 Identification list for *Sclerocyphon* in samples from the Thomson River and associated rivers and streams collected in 1979-1980 as part of the Gippsland Rivers Environmental Survey

Date	Site	Sample (No. of animals)	Identification		
			Sclerocyphon striatus Lea	*Sclerocyphon maculatus* Blkb.	*Sclerocyphon zwicki* sp.n
27/11/79	T6	QS3 (2)		2E	
		QS7 (3)		3E	
	Thomson-Jordan Divide Rd.	QS8 (1)		1E	
		QS9 (3)		3E	
		C5 (1)		1E	
		C6 (1)		1E	
	T13a	QS1 (1)			1E
		QS6 (1)			1E
	Knappings clearing 26-xi-1979	QS8 (2)	1E, 1L		
		QS9 (1)	1E		
		QS10(1)	1E		
		C8 (2)	1E, 1L		
		B7 (1)	1E		
		B10 (1)	1E		
	T15	QS1 (1)	1L		
	Low Saddle Track 25-xi-1979	QS2 (2)	2E		
		QS6 (2)	2E		
		QS7 (1)	1E		
		QS8 (3)	3E		
		QS10(3)	2E		1E
	T16	QS7 (3)	3E		
	7 km NNW Walhalla (Narrows Gauging Station) 22-xi-1979	QS8 (2)	2E		
		QS9 (4)	4E		
		QS10(2)	1L		1L
		C4 (1)	1E		
	T21a Forestry Track T6 Thomson-Jordan Divide Rd.	QS9 (1)	1L		
		QS8 (1)	1E		
		QS10(3)	2E	1E	
		B10 (3)	3E		

Table A-2 (cont'd)

Date	Site	Sample (No. of animals)	Identification		
			Sclerocyphon striatus Lea	*Sclerocyphon maculatus* Blkb.	*Sclerocyphon zwicki* sp.n
6/3/80	T13a	C4 (1)	1E		
	Knappings clearing	C6 (1)	1E		
		C7 (1)	1E		
		C8 (2)	2E		
		B9 (2)	2E		
7/3/80	T14a	QS7 (1)	1E		
	11 km NNW Walhalla	B6 (1)	1E		
		B7 (1)	1E		
		B8 (3)	2E, 1L		
		B10 (2)	2E, 1L		2E
6/3/80	T13a	QS2 (1)			1E
	Knappings clearing	QS6 (1)	1E		
		QS7 (2)	1E, 1L		
		QS9 (2)	1E, 1L		
		QS10(1)			1E
10/3/80	T15	QS1 (1)			1E
	Low Saddle Track	QS2 (2)	1E		
		QS3 (4)	4E		
		QS4 (1)	1E		
		QS5 (2)	2E		
		QS6 (1)	1E		
		QS10(2)	1E		

Table A-2 (cont'd)

Date	Site	Sample (No. of animals)	Identification		
			Sclerocyphon striatus Lea	Sclerocyphon maculatus Blkb.	Sclerocypho zwicki sp.n
4/3/80	T16	QS3 (1)	1E		
	7 km NNW Walhalla	QS4 (2)	1E		1E
	(Narrows gauging Stat^{n})	QS5 (1)	1E		
		QS6 (2)	1E		1E
		QS7 (1)	1E		
		QS8 (1)	1E		
		QS10 (1)	1E		
		C4 (1)	1E		
		C5 (4)	2E		2E
		C7 (1)	1E		
		B6 (3)	3E		
		B7 (1)	1E		
		B10 (1)	1E		
5/3/80	T21a	QS3 (1)	1E		
		QS4 (1)	1E		
	Forestry Track	QS5 (1)			1E
		QS6 (1) *1			
		C4 (1)	1E		
		C6 (9)	8E		1E
		C8 (1)			1E
		B6 (56)	56E		
		B7 (41)	41E		
		B8 (4)	4E		
		B9 (4)	2E, 1L		1E
		B10 (1)	1E		
May/June 1980	T6	QS6 (1)		1E	
	Thomson-Jordan Divide Rd 1/6/1980	QS8 (2)		2E	

*1 No larva present, only mites

Table A-2 (cont'd)

Date	Site	Sample (No. of animals)	Identification		
			Sclerocyphon striatus Lea	*Sclerocyphon maculatus* Blkb.	*Sclerocyphon zwicki* sp.n
May/June 1980					
	T13a	QS10 (2) *2	2E		
	30/5/80	B7 (1)	1E		
		B8 (1)	1E		
	Knappings clearing 2/6/1980	B9 (3)	2E		1E
	T14a	QS1 (1)			1E
		QS2 (3)	2E		1E
		QS3 (1)	1L		
		QS5 (1)			1E
		QS9 (1)	1E		
	T15	QS1 (1)			1E
	Low saddle track.	QS2 (1)	1E		
	27/5/1980	QS4 (1)			1E
		QS6 (2)			2E
		QS8 (3)	1E, 1L		1E
		QS9 (2)	1E, 1L		
		QS10 (3)	2E, 1L		
	T16	QS1 (1)	1E		
	7 km NNW Walhalla (Narrows gauging stat^{n}).	QS6 (1)	1E		
		QS7 (2)	2E		
	29-v-1980	QS9 (2)	2E		

*2 Not labelled as QS10

Table A-2 (cont'd)

Date	Site	Sample (No. of animals)	Identification		
			Sclerocyphon striatus Lea	*Sclerocyphon maculatus* Blkb.	*Sclerocyphon zwicki* sp.n
May/June 1980	T16	B6 (2)	2E		
	7 km NNW Walhalla (Narrows gauging Stat^{n})	B8 (1)	1E		
		B9 (1)	1E		
	T21a	QS3 (1)	1E		
	Forestry Track C6	QS7 (2)	2E		
	28-v-1980.	B6 (2)	2E		
		B7 (1)	1E		
		B9 (1)	1E		

Table A-3 Identification list for *Sclerocyphon* in samples from the Mitta Mitta River collected from 1976-1978 as part of the Dartmouth Environmental Survey

Locality	Date	Sample	No. specimens	Identification		
				S. striatus	S. zwicki	S. basicollis
Site 1A	3/11/77	KS2	1	1		
dam wall		KS3	1	1		
Site 1A	15/11/77	KS	7	7		
" "		BS1	1	1		
" "		BS2	1		1	
Site 1	2/11/77	KS	9	6		3
Site 1	15/11/77	KS1	3		1	2
" "		KS2	1		1	
" "		KS2 LOM	1	1		
" "		KS3	2	2		
Site 2A	3/11/77	KS2	2	2		
Site 2A	5/11/77	KS	2	2		
Site 2A	15/11/77	KS1	1	1		
" "		KS2	2	1	1	
Site 2	2/11/77	BS	1			1
Site 2	14/11/77	KS2	5	4		2
Site 3	3/11/77	KS	5	2		3
Site 3	14/11/77	KS1	2	2		
" "		KS2	8	7		1
" "		KS2 LOM	1	1		
" "		KS3	5	4	1	
Site IVA	2/11/77	KS	7	5	1	1
Site 4A	14/11/77	KS1	4	4		
" "		KS2	9	7		2
" "		KS2 LOM	2	2		
Site 4Aa	7/11/77	KS	1	1		
Site 4Aa	14/11/77	KS	4	3	1	
Site 4Aa	7/11/77	KS	12	11	1	
Site 5	7/11/77	KS1	2	1		1
Site 5	13/11/77	KS1	2	1		1
" "		KS2	2			2
" "		KS2 LOM	1			1
Site 7	11/11/77	KS	8	7	1	
" "		KS LOM	5	5		
" "		BS	1	1		

Table A-3 (cont'd)

Locality	Date	Sample	No.specimens	Identification		
				S.striatus	S.zwicki	S.basicollis
5 km u/s dam wall	6/11/76	KS1	1	1		
" "		KS2	10	9		1
" "		RA1	6	6		
" "		RB3	1	1		
Site I	5/11/76	RA3	2	2		
Site IA	5/11/76	RA1	2	2		
" "		RA2	2	2		
Site IIA " "	28/10/76	RA3	2	2		
Site III	4/11/76	RA3	1			1
" "		RB2	4	3		1
Site III	5/11/76	RA5	1	1		
Site IVA	2/11/76	RA2	4	4		
" "		RA3	7	7		
" "		RA4	4	4		
" "		RA5	6	6		
Site 5	3/11/76	RB1	2	1		1
" "		RC2	2	2		
$2\frac{1}{4}$ miles NW Eskdale	2/2/75		1	1		
Site IA	8/2/78	?	2	2		
Site II	8/2/78	KS1	8	6		4
" "		KS1 LOM	7	5		3
" "		KS2	1	1		
" "		BS	1	1		
" "		BS LOM	1	1		
Site III	9/2/78	KS1	13	7		6
Site IVA	9/2/78	KS1	1	1		
" "		KS1 LOM	1	1		
" "		KS3	3	2		1
" "		BS	1			1
" "		BS LOM	2	2		
Site V	10/2/78	KS1	1	1		
" "		KS1 LOM	4	4		
Site VII	10/2/78	KS1 LOM	1		1	
" "		KS2	2	2		

Table A-3 (cont'd)

Locality	Date	Sample	No. specimens	Identification		
				S. striatus	S. zwicki	S. basicoll.
Site C2	14/2/78	KS1	12	12		
dam wall		KS1 LOM	7	7		
Site C3	13/2/78	KS1	5	5		
" "		KS1 LOM	4	4		
" "		KS2	1	1		
Site O	6/3/77	KSL	69	67	2	
" "		BS2	1	1		
" "		RA1	17	17		
" "		RA2	11	11		
" "		RA3	1	1		
" "		RA4	2	1		1
" "		RA5	7	6	1	
" "		RB1	3	3		
" "		RC1	5	4	1	
" "		RC2	3	3		
" "		RC3	1	1		
" "		RC4	1	1		
Site IA	6/3/77	KS1	5	1	1	4
" "		KS1 pres.	6	6		
" "		BS1	3	3		
" "		BS2	2			2
Site I	7/3/77	?	1			1
" "		KS1	6	6		
" "		RA1	2	2		
" "		RA3	1	1		
" "		RC1	40	40		
" "		RC2	19	19		
" "		RC3	12	12		
" "		RC4	8	8		
Site V	5/3/77	KS2	23	23		
Site VII	7/3/77	KS3	8	6	2	

Table A-3 (cont'd)

Locality	Date	Sample	No.specimens	Identification		
				S.striatus	S.zwicki	S.basicollis
Site 0	2/11/77	KS	12	11		1
Site OA	2/11/77	KS	6	4	1	
Site C1	9/11/77	KS	1	1		
Site C2	8/11/77	KS	9	9		
Site C3	2/11/77	KS	13	13		
Site C3	9/11/77	KS	13	13		
dam wall		BS	1	1		
" "		BS	1	1		
Site II	27/10/78	KS1	5	4		1
dam wall		KS1 LOM	2	2		
" "		KS2	1	1		
" "		KS3	1	1		
" "		KS4	1			1
" "		KS6	2	2		
" "		KS6 LOM	2	2		
" "		KS7	1	1		
Site III	29/10/78	KS1	3	2		1
" "		KS3	1			1
" "		KS3 LOM	2	2		
Site 4A	28/10/78	KS1	1	1		
" "		KS2	1	1		
" "		KS2 LOM	1	1		

Table A-4 Identification list for Sclerocyphon in samples from the Latrobe River and associated rivers and streams collected in 1979 as part of Latrobe River and Traralgon Creek Survey.

Locality	Date	Sample	No. Specimens	Identification	
				S.maculatus	S.stria
Traralgon Creek 60	5/5/79	Q1	1	1	
		Q2	4	3	1
		Q4	1	1	
		Q5	1		1
		Q6	3	3	
		Q8	1	1	
		Q9	2	2	
		Q10	1	1	
Middle Creek S41		Q12	1	1	
		Q16	1		1
		Q18	1		1
		Q20	1		1
Little Morwell R. S39	6/5/79	Q24	1	1	
Tyers R. on Yallourn Nth-Tyers Rd S57	7/5/79	Q44	1		1
Eastern Tanjil R. at Tanjil Junction S33	8/5/79	Q71	1		1
		Q79 suppl.	1		1
Western Tyers R. on Xmas. Ck Rd. S52	9/5/79	Q81 suppl.	1	1	
		Q83 "	1	1	
		Q84	1	1	
		Q84 suppl.	1	1	
		Q87 suppl.	1	1	
		Q88 "	2	2	
Middle Tyers R above Tyers Junction S53	9/5/79	Q92	1		1
		Q92 suppl.	3	3	
		Q96	1	1	
		Q97	2	2	
		Q97 suppl.	4	4	
Western Tanjil on Saxtons Rd.	10/5/79	Q101 suppl.	1	1	

Table A-4 (cont'd)

Locality	Date	Sample	No. Specimens	Identification	
				S.maculatus	S.stri
LaTrobe R. at Hawthorn Ck. S15	10/5/79	Q111 suppl.	1	1	
		Q111	1		1
		Q112	1		1
		Q114	1		1
		Q116 suppl.	2	1	1
		Q117	1	1	
		Q120	1	1	
LaTrobe R on Powelltown Noojee Rd. S1	11/5/79	Q130 suppl.	1	1	
Loch R, 14.5 km N of Noojee S6	11/5/79	Q137	1	1	
		Q137 suppl.	5	5	
		Q138	1	1	
		Q138 suppl.	1	1	
		Q139 suppl.	1	1	
		Q140 suppl.	1	1	
Toorongo R 1 km S of Toorongo Rd S12	12/5/79	Q145 suppl.	1	1	
		Q147	2	2	
		Q147 suppl.	2	2	
		Q148	1	1	
Eastern Tanjil R at Tanjil Junction S33	8/5/79	BS16	1		1
Little Morwell R S39	6/5/79	BS5	1*		
		BS2	1	1	
LaTrobe R 9.8 km W of Noojee	17/5/79	BS28	1	1	
Tyers R at Walhalla Rd Bridge			1*		

1 * = S. basicollis

APPENDIX B

Tables of Mahalanobis distances compiled from the canonical variate analyses used to analyse differences in the shape of larval *Sclerocyphon* (as described in Chapter 5).

TABLE B-1 Mahalanobis distances for canonical variate analysis on covariance-adjusted data set (pilot study) using six variables.

1	0.00				
2	2.72	0.00			
3	3.75	2.43	0.00		
4	3.64	2.22	3.69	0.00	
5	2.80	2.47	3.51	3.77	0.00
6	4.53	2.56	2.99	3.15	4.92
7	5.53	3.70	4.78	3.00	5.77
8	3.29	2.01	3.93	1.06	3.56
9	2.95	2.00	3.53	1.75	3.26
10	5.88	4.38	5.70	3.33	5.72
11	4.45	3.54	5.13	2.20	3.86
12	3.94	2.54	4.38	1.42	3.46
13	5.10	3.79	5.41	2.83	4.11
14	4.19	3.55	5.61	2.79	3.58
15	3.01	2.96	5.00	2.60	2.99
	1	2	3	4	5
6	0.00				
7	2.42	0.00			
8	3.05	2.79	0.00		
9	3.15	3.06	1.31	0.00	
10	4.18	2.16	3.05	3.01	0.00
11	4.94	4.08	2.22	2.39	3.07
12	3.90	3.31	1.29	1.71	2.84
13	4.93	3.90	2.59	3.01	2.93
14	5.30	4.70	2.40	2.96	3.97
15	5.02	4.96	2.29	2.61	4.64
	6	7	8	9	10
11	0.00				
12	1.18	0.00			
13	1.59	1.82	0.00		
14	1.64	1.76	1.92	0.00	
15	2.31	2.06	3.17	1.55	0.00
	11	12	13	14	15

TABLE B-2 Mahalanobis distances for canonical variate analysis on total-length-adjusted data set (pilot study) using six variables.

1	0.00				
2	3.70	0.00			
3	3.82	1.84	0.00		
4	4.54	1.77	2.54	0.00	
5	2.66	1.86	3.08	2.38	0.00
6	5.34	2.26	2.08	3.07	4.05
7	6.37	3.02	3.50	2.88	4.39
8	4.35	1.46	2.76	0.98	1.97
9	4.04	1.87	2.62	1.73	2.12
10	6.63	3.78	4.59	3.09	4.42
11	5.29	3.41	4.44	2.15	2.96
12	5.00	2.46	3.71	1.55	2.45
13	5.60	3.29	4.54	2.30	3.15
14	5.32	3.61	5.08	2.90	2.84
15	4.11	3.28	4.66	3.01	1.92
	1	2	3	4	5
6	0.00				
7	2.25	0.00			
8	2.98	2.64	0.00		
9	3.17	2.84	1.42	0.00	
10	3.97	2.04	2.81	2.67	0.00
11	4.90	3.88	2.12	2.32	2.81
12	3.97	3.10	1.26	1.81	2.60
13	4.50	3.28	1.86	2.53	2.37
14	5.37	4.51	2.48	3.17	3.74
15	5.45	5.21	2.75	3.11	4.67
	6	7	8	9	10
11	0.00				
12	1.31	0.00			
13	1.35	1.44	0.00		
14	1.75	1.74	1.63	0.00	
15	2.44	2.33	2.92	1.77	0.00
	11	12	13	14	15

TABLE B-3 Mahalanobis distances for canonical variates analysis on total data set (41 groups) using six variables (one size and five shape variables)

1	0.00																			
2	3.55	0.00																		
3	3.73	2.10	0.00																	
4	4.67	2.28	3.51	0.00																
5	3.30	2.43	2.98	3.73	0.00															
6	5.03	2.46	3.08	3.20	4.77	0.00														
7	6.36	3.73	4.89	2.89	5.65	2.68	0.00													
8	4.41	2.12	3.76	1.08	3.57	3.05	2.58	0.00												
9	3.90	2.18	3.40	1.94	3.23	3.29	3.06	1.52	0.00											
10	6.65	4.33	5.60	3.14	5.47	4.40	2.20	2.80	2.82	0.00										
11	4.07	2.56	2.99	3.57	1.15	4.67	5.23	3.47	2.92	4.83	0.00									
12	3.18	4.00	4.11	5.54	2.52	6.18	7.63	5.45	5.23	7.75	3.57	0.00								
13	3.45	1.34	3.04	2.48	2.57	2.83	3.43	1.75	1.68	3.76	2.64	4.40	0.00							
14	2.89	1.53	2.68	2.38	2.91	2.69	3.52	1.92	1.43	3.98	3.00	4.49	1.11	0.00						
15	2.69	2.25	3.11	3.06	2.67	3.63	4.17	2.55	1.52	4.14	2.68	4.35	1.55	1.10	0.00					
16	1.31	3.21	3.31	4.16	3.41	4.28	5.48	3.83	3.21	5.84	3.88	4.07	2.90	2.16	1.96	0.00				
17	2.75	2.91	3.37	3.75	3.01	3.99	4.61	3.22	2.30	4.61	3.02	4.62	2.12	1.75	1.01	1.77	0.00			
18	2.47	3.86	4.11	4.82	3.89	4.74	5.56	4.30	3.28	5.62	4.06	4.89	3.18	2.64	1.91	1.64	1.38	0.00		
19	4.31	2.92	3.10	3.95	1.42	4.95	5.53	3.88	3.27	5.10	0.45	3.70	3.03	3.35	2.99	4.11	3.22	4.22	0.00	
20	6.52	4.62	5.66	3.84	5.98	4.13	2.17	3.39	3.01	1.64	5.40	8.13	3.95	3.90	4.02	5.54	4.33	5.07	5.64	0.00
21	3.49	1.00	2.26	1.91	2.95	2.17	3.14	1.70	1.51	3.78	2.91	4.64	1.27	0.87	1.79	2.85	2.44	3.41	3.26	3.87
22	3.77	2.16	3.67	1.93	3.88	2.70	2.80	1.32	1.50	3.37	3.93	5.41	1.74	1.36	2.12	3.15	2.84	3.58	4.33	3.37
23	5.82	4.18	5.70	3.59	5.55	4.12	2.56	2.87	2.66	2.17	5.22	7.42	3.37	3.43	3.57	5.08	4.09	4.68	5.55	1.74
24	5.84	4.33	5.85	3.13	5.11	4.99	3.28	2.57	2.51	1.83	4.74	7.14	3.53	3.67	3.63	5.22	4.18	5.00	5.07	2.52
25	3.75	2.67	3.95	2.99	3.03	3.95	3.75	2.26	1.27	3.24	2.78	5.05	1.64	1.80	1.23	3.10	1.77	2.73	3.10	3.32
26	5.57	5.17	6.33	4.31	6.00	5.42	4.12	3.74	3.18	3.33	5.76	7.73	4.26	3.94	3.72	4.78	3.99	4.27	6.06	2.76
27	2.95	1.72	1.94	2.71	2.99	2.57	3.82	2.54	2.01	4.43	3.01	4.52	1.78	0.99	1.56	2.07	1.82	2.70	3.27	4.27
28	1.52	2.98	3.36	4.28	1.96	5.01	6.13	4.02	3.40	6.11	2.76	2.32	2.91	2.70	2.26	2.08	2.51	2.71	2.99	6.23
29	3.06	4.66	5.18	5.46	2.94	6.94	7.73	5.28	4.95	7.36	3.84	2.31	4.57	4.58	4.14	3.96	4.39	4.57	4.02	7.80
30	4.04	4.86	3.88	6.05	5.18	4.93	7.73	5.28	4.95	7.36	5.16	5.98	4.74	4.09	3.83	3.16	3.24	2.83	5.15	6.19
31	7.00	4.41	5.67	3.78	5.88	3.93	1.79	3.34	3.32	1.42	5.24	8.08	3.91	4.19	4.46	6.15	4.90	5.81	5.49	1.53
32	7.10	4.63	5.89	3.89	5.88	4.36	2.15	3.41	3.39	1.13	5.20	8.17	4.01	4.35	4.51	6.24	4.89	5.85	5.44	1.54
33	1.95	2.62	3.17	4.13	1.86	4.47	5.64	3.70	3.27	5.80	2.61	2.75	2.30	2.35	2.03	1.98	2.02	2.52	2.85	5.88
34	4.12	1.73	2.93	1.26	3.57	2.30	2.49	1.16	1.28	3.09	3.38	5.39	1.76	1.42	2.23	3.41	2.89	3.89	3.74	3.28
35	5.50	3.81	5.50	2.43	3.90	5.23	4.13	2.44	2.54	2.85	3.46	6.03	3.45	3.65	3.60	5.09	4.18	5.28	3.75	4.05
36	5.04	2.81	4.34	1.58	3.51	4.17	3.30	1.41	1.88	2.57	3.18	5.59	2.53	2.85	3.07	4.63	3.80	4.92	3.56	3.66
37	5.79	3.68	4.98	2.71	3.77	4.98	3.88	2.46	2.88	2.81	3.28	6.08	3.18	3.73	3.77	5.29	4.17	5.44	3.59	4.08
38	5.53	3.91	5.52	2.99	3.82	5.54	4.60	2.65	3.18	3.57	3.69	5.71	3.40	3.94	3.94	5.33	4.53	5.58	4.05	4.79
39	4.31	3.36	4.98	2.92	3.30	5.27	4.96	2.62	2.82	4.31	3.52	4.65	3.03	3.29	3.27	4.40	4.06	4.81	3.94	5.14
40	3.89	1.83	3.03	1.51	2.60	3.77	4.17	1.90	2.29	4.24	2.74	4.15	2.36	2.36	2.85	3.76	3.62	4.60	3.14	4.96
41	3.39	2.94	2.70	3.57	1.82	5.08	6.01	3.89	3.53	5.88	2.15	2.92	3.50	3.32	3.24	3.54	3.64	4.40	2.29	6.40
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20

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20	
21	0.00
22	1.48
23	3.57
24	3.80
25	2.25
26	4.38
27	1.10
28	3.16
29	4.98
30	4.44
31	3.93
32	4.15
33	2.84
34	0.93
35	3.55
36	2.63
37	3.57
38	3.93
39	3.43
40	2.00
41	3.22
	21

TABLE B-3 (continued)

22	0.00																		
23	2.59	0.00																	
24	2.94	1.85	0.00																
25	2.20	2.79	2.65	0.00															
26	3.33	2.24	2.25	3.15	0.00														
27	2.15	4.16	4.39	2.46	4.55	0.00													
28	3.71	5.57	5.38	3.11	5.58	2.85	0.00												
29	5.28	6.97	6.31	4.59	6.75	4.86	2.25	0.00											
30	5.18	6.43	6.99	4.78	6.26	3.43	4.41	6.45	0.00										
31	3.63	2.18	2.87	3.66	3.95	4.60	6.50	8.00	6.88	0.00									
32	3.84	2.30	2.64	3.60	3.84	4.76	6.56	7.96	7.03	0.67	0.00								
33	3.49	5.30	5.24	2.82	5.51	2.46	1.23	3.00	4.12	6.07	6.11	0.00							
34	1.21	3.08	3.19	2.35	3.90	1.74	3.85	5.48	4.99	3.39	3.59	3.58	0.00						
35	3.41	3.82	2.32	2.91	4.05	4.12	4.70	5.24	7.01	4.04	3.80	4.70	3.08	0.00					
36	2.47	3.21	2.23	2.45	3.99	3.43	4.30	5.16	6.60	3.44	3.37	4.18	2.16	1.25	0.00				
37	3.64	3.99	2.78	2.98	4.60	4.14	4.93	5.58	7.03	3.78	3.47	4.58	3.21	1.46	1.60	0.00			
38	3.64	4.10	2.74	3.18	4.59	4.60	4.68	4.88	7.62	4.54	4.31	4.55	3.64	1.62	1.67	1.63	0.00		
39	3.03	4.10	3.15	2.90	4.43	4.07	3.55	3.74	7.02	5.10	5.05	3.79	3.35	2.42	2.07	3.02	1.82	0.00	
40	2.46	4.46	3.92	3.04	5.06	2.67	3.24	4.20	5.95	4.83	4.93	3.32	2.03	2.71	1.97	3.04	2.93	2.32	0.00
41	4.17	6.14	5.54	3.85	6.29	3.12	2.45	3.18	5.29	6.47	6.50	2.89	3.66	3.98	3.80	4.29	4.37	3.68	2.37	0.00
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41

TABLE B-4 Mahalanobis distances for canonical variates analysis performed on total data set (41 groups) using five variables (the five shape variables)

1	0.00																			
2	3.54	0.00																		
3	3.45	1.79	0.00																	
4	4.61	2.03	2.77	0.00																
5	2.64	1.75	2.92	2.53	0.00															
6	4.95	2.14	2.02	3.19	3.78	0.00														
7	6.07	2.97	3.60	2.65	4.08	2.49	0.00													
8	4.29	1.68	2.90	1.05	1.96	3.05	2.42	0.00												
9	3.65	1.99	2.76	1.93	1.94	3.27	2.77	1.47	0.00											
10	6.50	3.98	4.85	3.07	4.29	4.37	2.14	2.77	2.70	0.00										
11	3.42	1.72	2.88	2.02	1.14	3.48	3.24	1.37	0.87	3.23	0.00									
12	2.09	3.42	3.99	4.56	2.49	5.22	6.31	4.28	4.29	6.76	3.57	0.00								
13	3.45	1.27	2.62	2.40	1.45	2.72	2.93	1.53	1.62	3.54	1.24	3.60	0.00							
14	2.65	1.30	1.88	2.37	1.49	2.65	3.23	1.85	1.42	3.87	1.31	3.43	1.04	0.00						
15	2.68	2.21	2.72	3.00	1.63	3.54	3.77	2.40	1.45	3.94	1.35	3.55	1.55	1.03	0.00					
16	1.28	3.15	2.86	4.13	2.55	4.23	5.23	3.76	3.19	5.73	2.99	3.08	2.89	2.15	1.96	0.00				
17	2.74	2.90	3.12	3.65	2.37	3.85	4.13	3.02	2.18	4.34	2.21	4.03	2.10	1.63	0.97	1.73	0.00			
18	2.46	3.82	3.76	4.80	3.17	4.69	5.31	4.23	3.26	5.50	3.23	4.11	3.18	2.63	1.90	1.64	1.32	0.00		
19	3.43	1.81	2.86	2.08	1.29	3.47	3.21	1.46	0.70	3.16	0.21	3.69	1.30	1.27	1.22	2.95	2.08	3.11	0.00	
20	6.19	3.98	4.49	3.62	4.42	3.97	2.17	3.22	2.63	1.51	3.34	6.81	3.45	3.58	3.53	5.24	3.73	4.74	3.19	0.00
21	3.48	0.81	1.51	1.85	1.89	2.07	2.68	1.55	1.48	3.61	1.53	3.80	1.26	0.84	1.78	2.85	2.40	3.41	1.53	3.45
22	3.41	0.98	2.09	1.72	1.41	2.61	2.78	1.17	1.09	3.36	0.92	3.63	0.91	0.77	1.49	2.84	2.23	3.31	0.96	3.34
23	5.23	3.05	4.10	3.10	3.17	3.78	2.47	2.40	1.79	1.83	2.15	5.53	2.34	2.75	2.60	4.53	3.07	4.08	2.05	1.67
24	5.52	3.72	4.81	2.91	3.29	4.89	3.28	2.40	2.13	1.76	2.34	5.69	3.05	3.39	3.15	4.95	3.64	4.71	2.29	2.52
25	3.74	2.60	3.56	2.95	1.98	3.91	3.39	2.16	1.24	3.05	1.21	4.27	1.63	1.78	1.22	3.10	1.71	2.73	1.08	2.82
26	4.69	3.99	4.55	3.68	3.35	5.01	3.98	3.16	2.09	2.93	2.50	5.55	3.16	3.05	2.36	3.93	2.47	3.27	2.32	2.60
27	2.95	1.69	1.35	2.60	2.23	2.40	3.30	2.33	1.92	4.20	2.06	3.64	1.77	0.85	1.55	2.05	1.82	2.69	2.00	3.75
28	1.18	2.90	3.33	3.92	1.66	4.65	5.42	3.51	3.03	5.64	2.46	1.63	2.69	2.26	1.98	1.68	2.37	2.42	2.50	5.46
29	2.67	4.50	5.18	4.97	2.90	6.50	6.94	4.65	4.48	6.76	3.78	2.13	4.26	4.11	3.80	3.54	4.17	4.22	3.87	6.95
30	3.96	4.84	3.83	5.86	5.04	4.62	5.83	5.56	4.68	6.61	4.96	5.75	4.65	3.88	3.72	2.99	3.17	2.64	4.82	5.51
31	6.63	4.01	4.85	3.70	4.72	3.89	1.75	3.30	3.19	1.42	3.70	7.07	3.65	4.07	4.23	6.02	4.61	5.67	3.62	1.43
32	6.97	4.32	5.21	3.84	4.83	4.34	2.08	3.39	3.30	1.13	3.80	7.25	3.82	4.26	4.34	6.14	4.65	5.75	3.73	1.38
33	1.68	2.53	3.14	3.75	1.57	4.04	4.84	3.12	2.87	5.28	2.32	2.37	2.01	1.81	1.70	1.52	1.83	2.20	2.36	5.03
34	4.04	1.33	1.93	1.26	2.22	2.30	2.23	1.15	1.26	3.03	1.58	4.34	1.63	1.39	2.13	3.37	2.74	3.86	1.56	3.03
35	5.50	3.78	4.77	2.35	3.27	5.17	3.73	2.29	2.49	2.55	2.56	5.48	3.45	3.63	3.60	5.08	4.18	5.28	2.58	3.57
36	5.02	2.71	3.94	1.55	2.54	4.14	2.95	1.29	1.87	2.37	1.81	4.83	2.51	2.85	3.06	4.62	3.76	4.91	1.88	3.28
37	5.78	3.68	4.87	2.46	3.41	4.81	3.14	2.04	2.71	2.18	2.73	5.74	3.14	3.63	3.73	5.25	4.17	5.40	2.77	3.29
38	5.53	3.87	5.28	2.94	3.11	5.50	4.28	2.53	3.16	3.37	2.79	5.07	3.39	3.93	3.94	5.33	4.51	5.58	2.91	4.43
39	4.27	3.23	4.57	2.91	2.05	5.26	4.78	2.58	2.82	4.24	2.16	3.57	3.00	3.29	3.24	4.39	3.99	4.48	2.31	4.93
40	3.69	1.82	2.76	1.21	1.83	3.61	3.62	1.52	2.17	3.95	1.82	3.49	2.35	2.27	2.84	3.74	3.62	4.59	1.96	4.45
41	2.77	2.44	2.64	2.34	1.82	4.20	4.61	2.55	2.45	4.83	2.14	2.88	2.81	2.24	2.50	2.77	3.16	3.81	2.20	5.00
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21	0.00
22	0.64
23	2.75
24	3.42
25	2.25
26	3.44
27	1.06
28	2.91
29	4.65
30	4.31
31	3.73
32	4.01
33	2.54
34	0.77
35	3.55
36	2.62
37	3.51
38	3.93
39	3.42
40	1.96
41	2.33
	21

TABLE B-4 (continued)

22	0.00																		
23	2.42	0.00																	
24	2.92	1.74	0.00																
25	1.76	1.64	2.10	0.00															
26	3.04	2.19	1.97	1.65	0.00														
27	1.39	3.27	3.95	2.44	3.42	0.00													
28	2.67	4.32	4.54	2.85	3.93	2.68	0.00												
29	4.25	5.66	5.29	4.22	5.03	4.62	2.18	0.00											
30	4.59	5.50	6.44	4.65	5.00	3.34	4.40	6.40	0.00										
31	3.63	1.91	2.84	3.45	3.67	4.34	6.01	7.40	6.49	0.00									
32	3.83	1.96	2.58	3.45	3.47	4.56	6.14	7.42	6.69	0.65	0.00								
33	2.32	3.94	4.35	2.51	3.80	2.26	1.23	2.95	4.12	5.53	5.64	0.00							
34	0.88	2.53	2.99	2.30	3.22	1.54	3.42	4.97	4.74	3.31	3.55	3.11	0.00						
35	3.07	2.95	1.49	2.91	2.86	4.12	4.58	4.98	6.95	3.80	3.60	4.57	3.01	0.00					
36	2.16	2.39	1.65	2.45	3.05	3.40	4.07	4.79	6.49	3.26	3.24	3.94	2.13	1.39	0.00				
37	3.05	2.70	1.56	2.90	3.14	4.13	4.90	5.46	7.02	3.27	3.00	4.54	2.99	1.66	1.39	0.00			
38	3.36	3.36	2.14	3.18	3.66	4.60	4.53	4.56	7.56	4.35	4.16	4.39	3.59	1.62	1.66	1.51	0.00		
39	2.85	3.59	2.85	2.88	3.72	4.02	3.20	3.10	6.89	5.01	4.97	3.44	3.54	2.38	2.07	2.87	1.78	0.00	
40	1.71	3.55	3.36	3.00	3.97	2.67	3.14	3.97	5.91	4.54	4.70	3.21	1.79	2.69	1.89	3.03	2.91	2.20	0.00
41	2.16	4.17	3.96	3.12	3.89	2.45	2.24	3.14	5.15	5.46	5.60	2.72	2.42	3.39	2.97	4.00	3.80	2.67	1.54	0.00
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41

TABLE B-5 Mahalanobis distances for canonical variates analysis performed on *S. secretus* data set (34 groups) using six variables (one size and five shape variables)

1	0.00																			
2	3.57	0.00																		
3	3.90	2.16	0.00																	
4	4.57	2.28	3.58	0.00																
5	3.39	2.49	2.98	3.75	0.00															
6	5.09	2.50	3.21	3.24	4.87	0.00														
7	6.29	3.74	5.02	2.94	5.75	2.69	0.00													
8	4.31	2.18	3.90	1.09	3.68	3.11	2.60	0.00												
9	3.81	2.26	3.60	1.92	3.35	3.39	3.10	1.49	0.00											
10	6.51	4.33	5.70	3.13	5.54	4.42	2.22	2.75	2.78	0.00										
11	4.14	2.63	2.98	3.64	1.13	4.79	5.39	3.62	3.12	4.97	0.00									
12	3.33	4.01	4.08	5.51	2.48	6.24	7.67	5.49	5.26	7.74	3.50	0.00								
13	3.41	1.39	3.16	2.43	2.71	2.87	3.41	1.73	1.67	3.70	2.80	4.46	0.00							
14	2.86	1.61	2.90	2.33	3.04	2.76	3.49	1.86	1.41	3.89	3.17	4.57	1.09	0.00						
15	2.63	2.32	3.33	3.00	2.82	3.71	4.16	2.49	1.48	4.05	2.88	4.43	1.55	1.10	0.00					
16	1.30	3.23	3.53	4.06	3.51	4.34	5.42	3.74	3.13	5.71	3.98	4.18	2.86	2.13	1.92	0.00				
17	2.71	2.94	3.54	3.68	3.12	4.06	4.59	3.16	2.25	4.51	3.16	4.68	2.11	1.74	1.00	1.74	0.00			
18	2.45	3.91	4.35	4.74	4.03	4.81	5.50	4.21	3.21	5.48	4.22	5.02	3.16	2.62	1.88	1.63	1.39	0.00		
19	4.42	3.02	3.10	4.04	1.42	5.09	5.72	4.06	3.50	5.27	0.48	3.62	3.21	3.55	3.22	4.25	3.41	4.44	0.00	
20	6.43	4.70	5.88	3.89	6.13	4.21	2.21	3.38	3.04	1.64	5.63	8.19	3.95	3.89	4.01	5.46	4.31	4.98	5.91	0.00
21	3.47	1.02	2.41	1.88	3.03	2.22	3.14	1.70	1.56	3.75	3.02	4.67	1.25	0.90	1.81	2.83	2.44	3.41	3.40	3.92
22	3.74	2.34	3.97	1.99	4.09	2.85	2.79	1.34	1.52	3.29	4.18	5.55	1.81	1.40	2.13	3.12	2.85	3.52	4.61	3.31
23	5.82	4.43	6.06	3.77	5.85	4.33	2.69	3.00	2.81	2.25	5.60	7.62	3.53	3.54	3.66	5.09	4.18	4.66	5.97	1.76
24	5.75	4.51	6.12	3.27	5.34	5.15	3.40	2.66	2.58	1.91	5.05	7.26	3.62	3.71	3.64	5.15	4.18	4.90	5.42	2.54
25	3.68	2.77	4.15	2.96	3.21	4.05	3.76	2.23	1.26	3.17	3.03	5.13	1.67	1.79	1.21	3.03	1.75	2.66	3.39	3.32
26	5.64	5.52	6.82	4.58	6.41	5.75	4.35	3.96	3.45	3.49	6.24	8.03	4.53	4.18	3.94	4.90	4.21	4.34	6.58	2.90
27	2.95	1.71	2.09	2.65	3.03	2.62	3.81	2.51	2.03	4.38	3.08	4.53	1.75	1.04	1.61	2.09	1.84	2.75	3.37	4.32
28	1.54	3.00	3.47	4.20	2.02	5.08	6.12	3.97	3.37	6.03	2.80	2.40	2.91	2.71	2.26	2.10	2.51	2.75	3.07	6.23
29	3.09	4.72	5.28	5.43	3.01	7.04	7.77	5.29	4.94	7.31	3.89	2.44	4.63	4.62	4.16	3.99	4.40	4.60	4.09	7.82
30	4.02	4.75	3.88	5.91	5.11	4.87	6.31	5.71	4.80	6.83	5.10	5.92	4.63	4.02	3.79	3.16	3.20	2.91	5.12	6.15
31	6.90	4.42	5.77	3.78	5.96	3.92	1.77	3.31	3.31	1.45	5.39	8.09	3.86	4.13	4.41	6.05	4.84	5.71	5.68	1.56
32	6.98	4.62	5.98	3.88	5.95	4.34	2.14	3.37	3.36	1.14	5.34	8.16	3.95	4.27	4.45	6.12	4.81	5.73	5.61	1.56
33	1.98	2.60	3.22	4.04	1.91	4.50	5.62	3.65	3.23	5.71	2.64	2.80	2.29	2.35	2.04	2.00	2.02	2.58	2.91	5.87
34	4.06	1.76	3.08	1.25	3.64	2.37	2.51	1.15	1.30	3.05	3.51	5.40	1.72	1.39	2.21	3.35	2.85	3.85	3.89	3.32
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20

1	0.00
2	3.57 0.00
3	3.90 2.16 0.00
4	4.57 2.28 3.58 0.00
5	3.39 2.49 2.98 3.75 0.00
6	5.09 2.50 3.21 3.24 4.87 0.00
7	6.29 3.74 5.02 2.94 5.75 2.69 0.00
8	4.31 2.18 3.90 1.09 3.68 3.11 2.60 0.00
9	3.81 2.26 3.60 1.92 3.35 3.39 3.10 1.49 0.00
10	6.51 4.33 5.70 3.13 5.54 4.42 2.22 2.75 2.78 0.00
11	4.14 2.63 2.98 3.64 1.13 4.79 5.39 3.62 3.12 4.97 0.00
12	3.33 4.01 4.08 5.51 2.48 6.24 7.67 5.49 5.26 7.74 3.50 0.00
13	3.41 1.39 3.16 2.43 2.71 2.87 3.41 1.73 1.67 3.70 2.80 4.46 0.00
14	2.86 1.61 2.90 2.33 3.04 2.76 3.49 1.86 1.41 3.89 3.17 4.57 1.09 0.00
15	2.63 2.32 3.33 3.00 2.82 3.71 4.16 2.49 1.48 4.05 2.88 4.43 1.55 1.10 0.00
16	1.30 3.23 3.53 4.06 3.51 4.34 5.42 3.74 3.13 5.71 3.98 4.18 2.86 2.13 1.92 0.00
17	2.71 2.94 3.54 3.68 3.12 4.06 4.59 3.16 2.25 4.51 3.16 4.68 2.11 1.74 1.00 1.74 0.00
18	2.45 3.91 4.35 4.74 4.03 4.81 5.50 4.21 3.21 5.48 4.22 5.02 3.16 2.62 1.88 1.63 1.39 0.00
19	4.42 3.02 3.10 4.04 1.42 5.09 5.72 4.06 3.50 5.27 0.48 3.62 3.21 3.55 3.22 4.25 3.41 4.44 0.00
20	6.43 4.70 5.88 3.89 6.13 4.21 2.21 3.38 3.04 1.64 5.63 8.19 3.95 3.89 4.01 5.46 4.31 4.98 5.91 0.00
21	3.47 1.02 2.41 1.88 3.03 2.22 3.14 1.70 1.56 3.75 3.02 4.67 1.25 0.90 1.81 2.83 2.44 3.41 3.40 3.92 0.00
22	3.74 2.34 3.97 1.99 4.09 2.85 2.79 1.34 1.52 3.29 4.18 5.55 1.81 1.40 2.13 3.12 2.85 3.52 4.61 3.31 1.62
23	5.82 4.43 6.06 3.77 5.85 4.33 2.69 3.00 2.81 2.25 5.60 7.62 3.53 3.54 3.66 5.09 4.18 4.66 5.97 1.76 3.76
24	5.75 4.51 6.12 3.27 5.34 5.15 3.40 2.66 2.58 1.91 5.05 7.26 3.62 3.71 3.64 5.15 4.18 4.90 5.42 2.54 3.92
25	3.68 2.77 4.15 2.96 3.21 4.05 3.76 2.23 1.26 3.17 3.03 5.13 1.67 1.79 1.21 3.03 1.75 2.66 3.39 3.32 2.29
26	5.64 5.52 6.82 4.58 6.41 5.75 4.35 3.96 3.45 3.49 6.24 8.03 4.53 4.18 3.94 4.90 4.21 4.34 6.58 2.90 4.69
27	2.95 1.71 2.09 2.65 3.03 2.62 3.81 2.51 2.03 4.38 3.08 4.53 1.75 1.04 1.61 2.09 1.84 2.75 3.37 4.32 1.09
28	1.54 3.00 3.47 4.20 2.02 5.08 6.12 3.97 3.37 6.03 2.80 2.40 2.91 2.71 2.26 2.10 2.51 2.75 3.07 6.23 3.16
29	3.09 4.72 5.28 5.43 3.01 7.04 7.77 5.29 4.94 7.31 3.89 2.44 4.63 4.62 4.16 3.99 4.40 4.60 4.09 7.82 5.01
30	4.02 4.75 3.88 5.91 5.11 4.87 6.31 5.71 4.80 6.83 5.10 5.92 4.63 4.02 3.79 3.16 3.20 2.91 5.12 6.15 4.34
31	6.90 4.42 5.77 3.78 5.96 3.92 1.77 3.31 3.31 1.45 5.39 8.09 3.86 4.13 4.41 6.05 4.84 5.71 5.68 1.56 3.91
32	6.98 4.62 5.98 3.88 5.95 4.34 2.14 3.37 3.36 1.14 5.34 8.16 3.95 4.27 4.45 6.12 4.81 5.73 5.61 1.56 4.11
33	1.98 2.60 3.22 4.04 1.91 4.50 5.62 3.65 3.23 5.71 2.64 2.80 2.29 2.35 2.04 2.00 2.02 2.58 2.91 5.87 2.80
34	4.06 1.76 3.08 1.25 3.64 2.37 2.51 1.15 1.30 3.05 3.51 5.40 1.72 1.39 2.21 3.35 2.85 3.85 3.89 3.32 0.92
	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21

TABLE B-5 (continued)

22	0.00												
23	2.63	0.00											
24	2.93	1.88	0.00										
25	2.20	2.90	2.67	0.00									
26	3.48	2.30	2.29	3.37	0.00								
27	2.25	4.33	4.48	2.49	4.87	0.00							
28	3.76	5.67	5.39	3.11	5.78	2.85	0.00						
29	5.35	7.08	6.33	4.61	6.91	4.89	2.27	0.00					
30	5.14	6.48	6.96	4.72	6.46	3.35	4.36	6.41	0.00				
31	3.58	2.29	2.96	3.64	4.14	4.56	6.46	6.00	6.77	0.00			
32	3.77	2.39	2.72	3.56	4.01	4.71	6.50	7.93	6.90	0.67	0.00		
33	3.54	5.42	5.27	2.83	5.74	2.43	1.23	3.05	4.04	6.02	6.04	0.00	
34	1.30	3.25	3.30	2.35	4.19	1.72	3.82	5.49	4.89	3.37	3.55	3.53	0.00
	22	23	24	25	26	27	28	29	30	31	32	33	34

TABLE B-6 Mahalanobis distances for canonical variates analysis performed on *S. secretus* data set (34 groups) using five variables (the five shape variables).

1	0.00																			
2	3.54	0.00																		
3	3.49	1.76	0.00																	
4	4.53	2.00	2.72	0.00																
5	2.58	1.81	2.94	2.51	0.00															
6	5.03	2.19	2.05	3.24	3.89	0.00														
7	6.02	2.94	3.53	2.67	4.10	2.45	0.00													
8	4.21	1.66	2.85	1.04	1.95	3.10	2.44	0.00												
9	3.77	2.00	2.76	1.92	1.89	3.38	2.83	1.45	0.00											
10	6.36	3.90	4.76	3.03	4.21	4.36	2.18	2.71	2.65	0.00										
11	3.34	1.77	2.90	2.02	1.11	3.60	3.29	1.37	0.85	3.16	0.00									
12	2.06	3.41	3.99	4.48	2.44	5.27	6.26	4.21	4.20	6.62	3.49	0.00								
13	3.41	1.27	2.60	2.37	1.48	2.79	2.91	1.51	1.60	3.45	1.25	3.57	0.00							
14	2.82	1.30	1.89	2.33	1.49	2.75	3.21	1.80	1.40	3.78	1.31	3.39	1.02	0.00						
15	2.63	2.24	2.76	2.97	1.60	3.66	3.80	2.36	1.41	3.85	1.32	3.49	1.55	1.05	0.00					
16	1.27	3.14	2.90	4.05	2.50	4.31	5.18	3.68	3.12	5.59	2.92	3.04	2.85	2.12	1.91	0.00				
17	2.70	2.92	3.16	3.61	2.34	3.96	4.14	2.97	2.14	4.24	2.17	3.98	2.09	1.64	0.96	1.70	0.00			
18	2.42	3.82	3.81	4.74	3.11	4.80	5.29	4.17	3.20	5.38	3.17	4.05	3.15	2.62	1.87	1.62	1.30	0.00		
19	3.35	1.85	2.88	2.08	1.25	3.59	3.26	1.46	0.69	3.09	0.21	3.61	1.31	1.27	1.20	2.88	2.05	3.05	0.00	
20	6.07	3.91	4.42	3.57	4.34	3.97	2.19	3.16	2.60	1.47	3.29	6.69	3.37	3.51	3.47	5.14	3.66	4.65	3.15	0.00
21	3.47	0.80	1.49	1.82	1.91	2.14	2.66	1.51	1.50	3.54	1.57	3.77	1.24	0.84	1.81	2.83	2.42	3.41	1.57	3.38
22	3.36	0.99	2.08	1.69	1.42	2.70	2.79	1.14	1.08	3.29	0.95	3.58	0.90	0.75	1.50	2.80	2.22	3.28	0.98	3.27
23	5.13	3.02	4.07	3.09	3.12	3.63	2.53	2.37	1.77	1.80	2.12	5.42	2.29	2.70	2.55	4.44	3.01	4.00	2.03	1.65
24	5.38	3.72	4.79	2.92	3.22	4.98	3.39	2.41	2.10	1.79	2.30	5.57	3.03	3.34	3.08	4.83	3.55	4.59	2.25	2.53
25	3.66	2.64	3.59	2.95	1.95	4.03	3.46	2.16	1.24	3.00	1.21	4.20	1.65	1.79	1.19	3.03	1.68	2.66	1.08	2.80
26	4.59	4.03	4.60	3.70	3.31	5.15	4.10	3.18	2.12	2.94	2.49	5.45	3.18	3.07	2.34	3.85	2.44	3.20	2.32	2.65
27	2.95	1.67	1.36	2.54	2.23	2.47	3.26	2.27	1.90	4.10	2.06	3.81	1.74	0.85	1.58	2.05	1.84	2.71	2.00	3.67
28	1.16	2.95	3.39	3.88	1.64	4.77	5.42	3.47	2.97	5.53	2.42	1.80	2.70	2.28	1.96	1.67	2.86	2.39	2.45	5.38
29	2.67	4.60	5.28	4.99	2.94	6.67	6.99	4.68	4.47	6.70	3.78	2.19	4.34	4.17	3.81	3.56	4.17	4.19	3.87	6.90
30	3.92	4.73	3.78	5.72	4.94	4.59	5.70	5.42	4.58	6.44	4.85	5.67	4.53	3.79	3.65	2.95	3.11	2.64	4.72	5.37
31	6.73	3.93	4.76	3.67	4.66	3.84	1.74	3.26	3.17	1.44	3.67	6.96	3.58	3.99	4.19	5.92	4.55	5.60	3.61	1.43
32	6.85	4.24	5.11	3.80	4.76	4.30	2.08	3.34	3.27	1.14	3.76	7.13	3.74	4.17	4.27	6.02	4.57	5.65	3.69	1.35
33	1.66	2.54	3.15	3.69	1.54	4.12	4.81	3.06	2.79	5.15	2.26	2.35	1.99	1.79	1.65	1.49	1.60	2.15	2.29	4.92
34	4.00	1.31	1.90	1.25	2.22	2.37	2.23	1.12	1.29	2.97	1.61	4.29	1.61	1.37	2.14	3.32	2.73	3.83	1.59	2.99
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20

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20	
21	0.00
22	0.64
23	2.72
24	3.42
25	2.28
26	3.49
27	1.05
28	2.94
29	4.72
30	4.21
31	3.66
32	3.93
33	2.52
34	0.75
	21

TABLE B-6 (continued)

22	0.00												
23	2.38	0.00											
24	2.90	1.75	0.00										
25	1.78	1.62	2.05	0.00									
26	3.07	2.24	1.94	1.64	0.00								
27	1.37	3.22	3.90	2.44	3.44	0.00							
28	2.67	4.25	4.43	2.80	3.86	2.71	0.00						
29	4.30	5.63	5.21	4.20	4.95	4.69	2.20	0.00					
30	4.48	5.37	6.30	4.56	4.93	3.26	4.36	6.38	0.00				
31	3.57	1.92	2.91	3.45	3.74	4.25	5.94	7.39	6.33	0.00			
32	3.76	1.94	2.63	3.42	3.52	4.47	6.05	7.38	6.52	0.65	0.00		
33	2.28	3.85	4.24	2.45	3.73	2.24	1.23	3.01	4.03	5.43	5.53	0.00	
34	0.88	2.51	3.00	2.33	3.28	1.50	3.42	5.02	4.63	3.26	3.49	3.07	0.00
	22	23	24	25	26	27	28	29	30	31	32	33	34

APPENDIX C

Supporting papers.*

(a) SMITH, J.A. and DARTNALL, A.J. (1980). Boundary layer control by Water Pennies (Coleoptera: Psephenidae). *Aquatic Insects*, 2(2): 65-72.
http://dx.doi.org/10.1080/01650428009361008

(b) SMITH, J.A. (1981). Two Tasmanian species of *Sclerocyphon* Blackburn (Coleoptera:Psephenidae) with notes on their life history and distribution. *Journal of the Australian Entomological Society*, 20: 277-288.
http://dx.doi.org/10.1111/j.1440-6055.1981.tb01048.x

* These papers were written by the present author under her married name.